# Conservation of diverse parasitoid assemblages across agricultural mosaics within the Cape Floristic Region, South Africa

by

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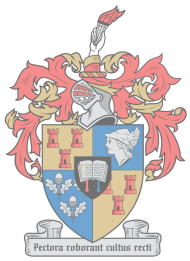


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## Declaration

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## General summary

The ever-growing agricultural industry within the Cape Floristic Region (CFR) threatens many arthropod species, including functionally beneficial insects such as parasitoids. Damage caused by insect pests within agricultural landscapes may be reduced by these important natural enemies. Various other vital ecosystem services and functions may be provided by maintaining structurally diverse agricultural landscapes as habitat heterogeneity promotes biodiversity. Here, I aim to investigate changes in parasitoid assemblages between various biotopes and across seasons within the CFR winelands.

Firstly, I assess whether parasitoid richness and assemblage structure differs between five dominant biotope types within CFR agricultural mosaics. I also investigate which environmental variables influence changes in diversity. The biotopes were vineyards, old fields, riparian vegetation, remnant natural vegetation, and areas invaded by alien trees. I found that parasitoid assemblage structure differed significantly among all biotopes, with the undisturbed habitats supporting highest parasitoid diversity. Each biotope type made a unique contribution to overall parasitoid diversity. Structural diversity and botanical diversity, as well as the amount of untransformed habitat in the landscape, influenced parasitoids. Various spatial scales are therefore important when conserving these organisms. By maintaining a diversity of biotope types, farmers will be able to promote parasitoid biodiversity across farmland mosaics.

Secondly, I assess the changing parasitoid assemblage structure and diversity across these biotope types over three seasons. Sample seasons were autumn, spring and summer. I found that parasitoid assemblage structure differed between the biotope types across the three seasons, with different biotopes having differential importance between seasons. Spatial and temporal turnover of species therefore takes place across agricultural landscapes in response to changing environmental conditions across various seasons.

It is therefore necessary for farmers to preserve a variety of biotope types to promote species movement and re-establishment throughout farmland mosaics. To conserve these functionally important insects, we need to consider movement of parasitoids throughout landscapes, and over larger spatial and temporal time-scales. Here I show that habitat

heterogeneity is an important consideration for future farmland design and planning for human-induced disturbances.

## Algemene opsomming

Die steeds groeiende landboubedryf in die Kaapse Floristiese Streek bedreig groot hoeveelhede geleedpotige spesies, insluitende voordelige insekte soos parasitoïede. Skade wat veroorsaak word deur insekteplae in landboulandskappe kan deur hierdie belangrike natuurlike vyande verminder word. Verskeie ander belangrike ekosisteemdienste en -funksies kan voorsien word deur die handhawing van uiteenlopende landboulandskappe, aangesien habitat-heterogeniteit biodiversiteit bevorder. Hier ondersoek ek die verandering in parasitoïede samestellings tussen verskillende biotope en oor seisoene binne die CFR-wynlande.

Eerstens het ek vasgestel of die parasitoïede rykheid en samestellingstruktuur verskil tussen vyf dominante biotoopsoorte binne CFR-landboumosaïeke. Ek het ook ondersoek ingestel na watter omgewingsveranderlikes veranderinge in diversiteit beïnvloed het. Die biotope was wingerde, ou velde, oewerplantegroei, oorblywende natuurlike plantegroei en gebiede wat deur indringerbome oorgeneem is. Parasitoïede samestellingstruktuur het aansienlik verskil tussen alle biotope, met die onverstoorde habitatte wat die hoogste parasitoïede diversiteit ondersteun. Elke biotooptipe het 'n unieke bydrae gelewer tot die algehele parasitoïede diversiteit. Strukturele diversiteit en botaniese diversiteit, sowel as die hoeveelheid ongetransformeerde habitatte in die landskap, het parasitoïede beïnvloed. Verskeie ruimtelike skale is dus belangrik wanneer hierdie organismes bewaar word. Deur die verskaffing van 'n verskeidenheid biotooptipes, kan boere volhoubare parasitoïede bevolkings oor landmosaïeke bevorder.

Tweedens, oor drie seisoene, het ek die veranderende parasitoïede samestellingstruktuur en diversiteit oor bogenoemde biotoopsoorte geassesseer. Steekproefseisoene was herfs, lente en somer. Parasitoïede samestellingstrukture het tussen die drie seisoene tussen die biotoopsoorte verskil. Ruimtelike en temporale omset van spesies vind dus plaas binne landboulandskappe in reaksie op veranderende omgewingstoestande oor verskillende seisoene.

Om af te sluit, dit is nodig vir boere om 'n verskeidenheid biotope te bewaar ten einde spesiebeweging te bevorder in landskappe. Navorsing gefokus op die beweging van voordelige natuurlike vyande dwarsdeur landskappe, en oor langer tydskale, kan toekomstige

landbougrondontwerp beïnvloed en beplanning van mensgeïnduseerde versteurings beïnvloed.

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# Chapter 1

## 1.1 General Introduction

### *1.1.1 Agriculture in the Cape Floristic Region*

The Cape Floristic Region (CFR) is a global biodiversity hotspot, situated in the south-western part of South Africa (Cowling et al., 2003; Mittermeier et al., 2004). Myers et al. (2000) classified biodiversity hotspots as areas with exceptionally high concentrations of endemic species that are suffering great losses of habitat. Of the world's six floral kingdoms, the CFR is the smallest, covering approximately 90 000 km² (Takhatajan, 1986). This small region, however, houses over 9000 plant species, with 70% classified as endemic (Goldblatt and Manning, 2000) and with insect diversity and endemism believed to be equally high (Procheş and Cowling, 2006).

The CFR experiences a Mediterranean climate and is therefore part of one of the rarest terrestrial biomes on Earth (Cowling et al., 1996), home to remarkably high levels of diversity (Myers et al., 2000) and housing more than 20% of the Earth's vascular plant taxa, including many rare and endemic species (Greuter, 1994). This biome possesses ideal conditions for agriculture (Fairbanks et al., 2004) and as a result agricultural expansion and intensification have been identified as significant drivers of widespread biodiversity loss (Norris, 2008). In 2003, Rouget et al., stated that 30% of the CFR had already been transformed, of which 25.9% was transformed by agricultural practices. In South Africa, vineyards are estimated to cover 110 000 ha of land, of which over 90% is found within the CFR (Rogers, 2006). Furthermore, as of 2001, up to 85% of West and South coast renosterveld shrubland had been replaced by vineyards, irrigated pastures and wheat fields (Reyers et al., 2001). This is alarming for the future of this biodiverse region as wine production in South Africa has increased steadily over the past century and is expected to continue to do so (Fairbanks et al., 2004).

### *1.1.2 Biodiversity and ecosystem services*

Various ecosystem services and processes rely on biodiversity within agricultural systems (Macfadyen et al., 2012). Ecosystem services, defined as "all of the conditions and processes by which ecosystems sustain and fulfil human life" (Daily, 1997), are separated into four categories; supporting services, provisioning services, regulating services and cultural services

(Altieri, 1999; Bugg et al., 1998; Nicholls and Altieri, 2004). Important services for agriculture include pest control, recycling of nutrients, regulation of local hydrological processes, control of local microclimates and detoxification of toxic chemicals (Altieri, 1999). Habitat management within agricultural systems aims to enhance pest regulation by promoting both habitat and arthropod diversity (Fiedler et al., 2008). Biological control of pests may reduce the need for external chemical inputs, saving money and ultimately preventing the consequential environmental costs of pesticide use such as decreased soil, water and food quality (Altieri, 1999).

Where alternative hosts and prey species are present, predator abundance may increase, promoting the control of insect pests (Bianchi and van der Werf, 2004; Östman, 2004). A diversity of plants may thus provide vital sources of food and shelter for predators (Zebnder et al., 2007). Furthermore, it has been shown that natural enemies that hibernate in nearby non-crop habitats, may inhibit the increase of pest populations within crops (Collins et al., 2002). The preservation of natural enemy populations within farmlands is thus highly connected with biodiversity (Gurr et al., 2003) and holds great benefits for both farm managers and the environment (Östman et al., 2003).

### *1.1.3 Agricultural landscape heterogeneity*

Agricultural landscapes range from severely homogenized farmlands to a diversity of biotopes and land-uses (Fahrig et al., 2011; Tilman et al., 2001). Vineyards have the potential to homogenize previously diverse agricultural landscapes and consequently reduce overall species turnover and local diversity. A variety of uncultivated habitats may provide support for biodiversity as well as protection against local extinction (Kehinde and Samways, 2014). Different biotope types are favoured by different species due to the various resources that they have to offer (Bianchi et al., 2006). Arthropod species that utilize various habitat types may benefit from diverse mosaics as they are able to move across the landscape and obtain resources from various patch types (Cunningham et al., 2013; Mandelik et al., 2012). This dispersal between various biotope types increases functional connectivity within agricultural landscapes. Improved dispersal within diverse mosaics may thus aid with alleviating the consequences of fragmentation and isolation (Driscoll et al., 2013; Fischer et al., 2006).

The long-standing conflict between agricultural production and biodiversity protection has brought about the land sparing versus land sharing debate (Tscharntke et al., 2012; Fischer et al., 2014). Land sparing, whereby land that is important for biodiversity is protected and kept separate from land used for production (Ekroos et al., 2016), has been criticised for neglecting vital biodiversity (Troupin and Carmel, 2014) and ecosystem services (Bommarco et al., 2013) found within agricultural land. Land sharing constitutes interventions within farmlands aimed at benefitting biodiversity and ultimately reducing agricultural intensity (Ekroos et al., 2016). The debate between integration versus segregation of agricultural production and biodiversity conservation often overlooks the important element of spatial scale (Fischer et al., 2014). Where some researchers have argued the importance of land sparing across large regions (Phalan et al., 2011), others have stressed the importance of sparing smaller areas for biodiversity conservation (Gabriel et al., 2013). Ekroos et al. (2016) suggested that sparing land at various spatial scales may allow for the preservation of important ecological processes, protecting important species both locally and regionally. Various habitat types therefore need to be preserved within and near farmlands, and across various spatial scales.

Of the various habitat types that occur within farmland mosaics, remnant natural patches are highly important as they often serve as vital refuges for native species (Phalan et al., 2011). Alternative habitats, such as natural remnants, may help maintain resilience within farmlands, preserving essential ecosystem functions during or after disturbance (Lin, 2011). This occurs where species that are functionally redundant at a certain point in time become important in response to environmental change. Greater species diversity therefore ensures the presence of such potentially important species (Vandermeer et al., 1998).

### *1.1.4 Hymenopteran parasitoids*

Hymenopteran parasitoids, referred to as parasitoids from here onwards, are functionally important organisms in natural as well as human modified environments. They make up more than 75% of the Hymenopteran order with approximately 240 000 species (Bonet, 2009) and are known to occupy a wide range of habitat types (Shaw, 2006). Parasitoids exhibit a feeding behaviour that is intermediate between a parasite (which harms but generally does not kill its host) and a predator (typically kill their host or prey) (Bonet, 2009; Dellinger and Day, 2014), which includes immature stages, eventually leading to the hosts' death. All parasitoid

species live part of their life-cycle developing inside or on the outside of their host (Dellinger and Day, 2014). These organisms attack a wide range of insect hosts, as well as other arthropods such as ticks and spiders. They are also known to target less desirable insects, such as pests that feed on valuable crops and are thus highly important in agriculture (Matos et al., 2016). Their role as biological control agents thus makes parasitoids highly valuable within agroecosystems (Shaw and Hochberg, 2001).

Parasitoids require the presence of host species for their reproduction, feeding and ultimately, survival. For example, where mealybug parasitoids are concerned, adults lay their eggs inside their prey, after which larva develop within their host before they eventually emerge as an adult (Daane et al., 2008). Additionally, for various species, adults are dependent on floral resources as alternative sources of food and habitat (Campos et al., 2006; Scarratt et al., 2008). Although some species are classified as generalists, where a number of different hosts are targeted, many are specialized to only one or two host species (Bonet, 2009). In general, parasitoids are however known to be exceptionally specialized (Shaw, 2006). Due to their occupying high tropic levels and tendency towards specialization, these organisms are highly sensitive to changes in prey abundance, floral resources, microclimate conditions and nesting areas (Matos et al., 2016), making them particularly vulnerable to extinction (Shaw, 2006; Shaw and Hochberg, 2001). Habitat transformation such as in the case of agricultural expansion and intensification may thus impose severe consequences for these beneficial insects (Landis et al., 2000).

### *1.1.5 Parasitoids within agricultural landscapes*

The regulation of insect pests by natural enemies is beneficial towards agricultural systems and is dependent on farmland biodiversity (Gonthier et al., 2014; Landis et al., 2000; Pak et al., 2015). Insect parasitoids hold the potential to regulate populations of many insect pests within agricultural landscapes (Pak et al., 2015; Pereira et al., 2007). Many agricultural landscapes that possess a simplified physical structure may however be unfavourable towards certain parasitoid species that require resources from non-crop habitats (Bianchi et al., 2005; Gagic et al., 2011; Landis and Menalled, 1998). Structurally diverse habitats may therefore be essential for the provision of refuges for natural enemies (Marino and Landis, 1996). Resources such as alternative hosts, food for adults (nectar and pollen), accessibility of overwintering habitats, constant food supply, and appropriate microclimates all support

increased parasitoid abundance (Landis et al., 2000; Menalled et al., 1999). Furthermore, it has been shown that increased vegetational structure results in higher insect diversity (Altieri et al., 2005; Danne et al., 2010). In support of this, parasitoid species richness has been found to be positively correlated with plant architectural complexity, such as vegetation structure and diversity (Fraser et al., 2007; Pak et al., 2015).

Parasitoid diversity and abundance in agroecosystems may be influenced by processes acting at various spatial scales (Menalled et al., 1999). This is because some parasitoids can forage over wide ranges. The entire landscape is therefore used by these organisms, and not just single patches. Biological diversity and ecological function are known to be influenced by habitat type and quality, as well as the spatial arrangement and connectivity of habitats within landscapes (Thies and Tscharntke, 1999). The fact that the spatial structure, habitat diversity and composition within agricultural landscapes varies from structurally diverse to homogenous landscapes, means that large-scale landscape effects may impact local biodiversity and ecological functions (Kruess, 2003). Agricultural intensification reduces overall landscape complexity, and as a result parasitoids are exposed to more fragmented resource availability (van Nouhuys, 2005).

In agricultural landscapes, sowing and harvesting causes vineyards to exhibit varying degrees of resource availability (Rand et al., 2006). During this time, high species diversity is necessary to sustain the pest control function of natural enemies. Species that were previously thought to be less crucial may become essential for biological control (Ives and Cardinale, 2004). This is known as the insurance hypothesis (Yachi and Loreau, 1999). Maintaining these redundant species is also important over longer time scales, especially in the face of climate change as high functional diversity gives an ecosystem a measure of resilience to disturbance (Tscharntke et al., 2007).

### *1.1.6 Parasitoids of the Cape Floristic Region*

In the past, most research within the CFR that focused on the effect of biological and ecological processes looked at precise habitats and not on the landscape structure as a whole. Kruess (2003) concluded that it is necessary to preserve large undisturbed habitats in order to maintain large populations of natural enemies such as parasitoids. He went on to conclude that it is highly likely that herbivores suffer more from parasitism in structurally rich

landscapes, and landscapes with a high proportion of large, undisturbed habitats. Additionally, Shaw and Hochberg (2001) highlighted that the poor knowledge of parasitic Hymenoptera is problematic in the field of conservation. More research is needed about parasitic wasps, both taxonomically and biologically.

There are gaps in the knowledge of farmland biodiversity within the CFR, especially with relation to the importance of farmland heterogeneity. Previous research has however shown that natural remnants within agroecosystems support species-rich and distinct parasitoid assemblages compared to vineyard (Gaigher et al., 2015). The value of conserving these habitat fragments for maintaining biodiversity within agricultural landscapes has been highlighted by various studies (Gaigher et al., 2015; Kehinde and Samways, 2012; Vrdoljak and Samways, 2014).

### *1.1.7 Study Area*

Many Mediterranean regions consist of small remnants of natural habitats that are separated by agricultural and urban areas. These small remnants of natural habitats may allow for the persistence of endemic species within this species rich, yet fragmented biome (Cox and Underwood, 2011). The protection of remnant natural habitat patches is therefore essential for the conservation of large amounts of rare and endemic species. Furthermore, non-crop habitat types are known to be more stable and diverse environments over time, compared to annual, arable crops (Tscharntke et al., 2007) due to their provision of various important resources for parasitoids and arthropod predators, such as permanent plant cover that may be suitable during overwintering, refuges from disturbance, as well as various other resources (Cronin and Reeve, 2005; Bianchi et al., 2006).

Within CFR agricultural landscapes, small-scale biotopes such as old fields (defined as vineyards abandoned for economic reasons), riparian and alien tree-invaded areas also need to be taken into account when considering overall farmland biodiversity. It has been shown that old fields play an important role in maintaining arthropod natural enemy diversity within CFR farmland mosaics (Gaigher et al., 2016). Riparian ecosystems, which are among the most threatened habitats within the CFR, are known to provide areas of refuge, reproduction, resting and feeding for both terrestrial and aquatic arthropods (Maoela et al., 2016). Alien tree-invaded areas are considered to be a serious problem in the CFR as they significantly

impact movement activities of insects as well as threaten their habitats (Magoba and Samways, 2012). Invasive alien trees possess strong colonising abilities, owing to their success within the CFR (Holmes and Richardson, 1999).

### *1.1.8 Objectives and thesis outline*

It is evident that there is a need for biodiversity conservation within agricultural landscapes. In order to do this one needs to look into biodiversity patterns as well as the value of various landscape elements. Additionally, it is important to understand how landscape heterogeneity influences biodiversity and its associated services. It is for these reasons that I will be focusing on agricultural mosaics.

The objective of this study is to investigate parasitoid diversity and assemblage structure across agricultural mosaics within the Cape Floristic Region, which will allow me to gain an understanding of the importance of agricultural heterogeneity for future farmland design. For the first data chapter (Chapter 2) I will investigate how parasitoid diversity and assemblage structure differs between various biotope types within the agricultural mosaic and which environmental variables have an impact on these differences. I will then examine how parasitoid diversity and assemblage structure differs over time by comparing parasitoid assemblages over three seasons (Chapter 3). This will allow me to assess the value of the various biotopes across different seasons. Important findings will then be discussed and analysed in Chapter 4, with management recommendations for future farmland design that aims to preserve parasitoid biodiversity and the essential ecosystem services that they have to offer.

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# Chapter 2

## High parasitoid diversity is maintained in a diverse farmland mosaic within a biodiversity hotspot, South Africa


### Abstract

Agricultural expansion and intensification threatens arthropod biodiversity within farmlands, including beneficial insects such as parasitoids. Parasitoids are important natural enemies within agricultural landscapes as they may regulate insect pest populations, reducing crop damage. To investigate the diversity and distribution of parasitoids within compositionally diverse agricultural landscapes, I assessed whether parasitoid richness and assemblage structure differs between different dominant biotope types within agricultural mosaics in the Cape Floristic Region, South Africa. These biotopes were vineyards, old fields, riparian vegetation, remnant natural vegetation, and areas invaded by alien trees. I also investigated which environmental variables influenced changes in diversity. Parasitoid assemblage structure differed significantly among all the biotope types, showing that each biotope makes an important contribution to the landscape-scale biodiversity. The undisturbed habitats (remnant and riparian vegetation) supported the highest parasitoid diversity and number of unique species, whereas richness and uniqueness were lower in disturbed biotopes (vineyards and invaded areas). Semi-natural biotopes were intermediate between the natural and disturbed biotopes in both parasitoid species richness and assemblage structure. These biotopes may play an important role in increasing functional connectivity in the mosaic. Parasitoids were influenced by local-scale variables, such as structural complexity and botanical diversity, as well as landscape-scale variables, such as amount of untransformed habitat in the landscape. Diverse habitat mosaics are needed to support the various parasitoid species and families across the landscape. To preserve the high parasitoid diversity within farmlands, conservation efforts should aim to maintain as much habitat heterogeneity within agricultural landscapes.

## 2.1 Introduction

Agricultural production and biodiversity conservation are largely perceived as conflicting practices, with declines in the biodiversity of a variety of taxa being linked to agricultural intensification (Biesmeijer et al., 2006; Conrad et al., 2006; Butler, Vickery and Norris 2007). Biodiversity has declined in high-intensity agricultural ecosystems due to intensified resource use and increased applications of agrochemicals (Benton et al., 2003). In addition, habitat loss and fragmentation, as well as homogenization of farmland, have been major drivers of declines in farmland biodiversity (Atwood et al., 2008; Tilman et al., 2001). Biodiversity loss severely threatens ecosystem services provided in both natural and cultivated ecosystems (Rands et al., 2010; Thompson et al., 2011). Insect biodiversity within agroecosystems is particularly important due to the various ecosystem services that they provide (Altieri, 1999). Insects that can persist in agricultural landscapes and forage within or between various habitats can provide various essential ecosystem services such as pollination, nutrient cycling and pest control (Lundberg and Moberg, 2003). To alleviate some of the impacts of agriculture on functionally important insects, recent farmland conservation efforts have adopted a landscape perspective (Tscharntke et al., 2005). Habitat management within farmlands aimed at preserving biodiversity may thus sustain the provision of ecosystem services that are essential for agricultural production as well as for human well-being (Macfadyen et al., 2012).

Habitat management practices that focus on maintaining a mosaic of biotope types while reducing land-use intensity within farmlands may help preserve biodiversity in agricultural production systems (Benton et al., 2003; Ekroos et al., 2016). Different landscape elements can each contribute to overall landscape biodiversity (Vrdoljak and Samways, 2013). Conserved natural remnants have been shown to make an important contribution to the preservation of insect diversity (Attwood et al., 2008; Tscharntke et al., 2008). Furthermore, riparian habitats enhance the abundance and colonization of predators within adjacent crop fields (Nicholls et al., 2001). Managed semi-natural habitats such as field margins and hedgerows are necessary within agricultural landscapes as they provide continuous shelter and a food supply for many species (Pywell et al., 2005; Diekotter et al., 2010). However, not all biotopes necessarily act as suitable habitat. Magoba and Samways (2012) found that

vineyards and areas invaded by alien trees in the Cape Floristic Region (CFR) possessed very low arthropod species richness and abundance compared to natural habitats.

Although, CFR vineyards are able to support various arthropod species, and as long as management intensity is not too high, they are not as hostile as previously suspected (Gaigher and Samways, 2010; Kehinde and Samways, 2012). Each habitat type may therefore have unique value within the farmland mosaic. This means that it is necessary for agricultural landscapes to have habitat heterogeneity to preserve the various resources and microclimates that different biotope types provide for a diversity of insects, including parasitoids (Gaigher et al., 2016).

Parasitoids are of great ecological importance in all terrestrial ecosystems, because they are involved in numerous interactions and ecological processes (Shaw, 2006). In agroecosystems, parasitoids can benefit agricultural production, as they regulate insect pest populations within farmland (Bonet, 2009). The natural biological control of insect pests is both environmentally and economically beneficial, as it reduces the need for harmful chemical pesticides. Natural enemies operate at a high trophic level and are vulnerable to extinction when threatened by habitat transformation (Shaw, 2006). By promoting habitat heterogeneity within agricultural landscapes, farmers may potentially provide parasitoids with critical resources, such as nectar, pollen and alternative hosts, and undisturbed refuges, which are important for survival in disturbed landscapes, and which are needed during certain stages of their life-cycle, such as overwintering (Landis et al. 2000). Bianchi et al.'s (2006) meta-analysis found that in 74% of studies on biodiversity and response by natural pest control to agricultural landscape composition showed that diverse landscapes increased natural enemy diversity. Furthermore, ecosystem functions, including parasitoid activity, is greater within complex agricultural landscapes than in simpler landscapes (Menalled et al., 1999). The conservation of alternative habitats is therefore essential, such as wooded hedgerows and woodlots, which sustain populations of various parasitoid host species (Marino et al., 2006).

Parasitoid abundance and diversity in agroecosystems may be influenced by processes acting at various spatial scales (Menalled et al., 1999). The entire agricultural mosaic therefore needs to be taken into consideration, and not just single habitat patches. Additionally, large-scale landscape effects may influence biodiversity and ecological functions locally. This is due to

variations in habitat diversity, composition and spatial structure, throughout entire agricultural mosaics. Farmlands range from structurally diverse mosaics to cleared, homogenized landscapes (Kruess, 2003), with varying potential for supporting high levels of biodiversity. Consequently, it is important to understand how landscape structure influences biodiversity in different types of agricultural landscapes, to be able to predict the effects of future land-use change (Cunningham et al., 2013).

The Cape Floristic Region of South Africa is home to many plant and arthropod species, and is a biodiversity hotspot of high conservation priority (Cowling, 1990; Maoela et al., 2016; Pryke and Samways, 2008; Rouget et al., 2003; Vrdoljak and Samways, 2013). However, about 25% of the CFR has been transformed into agricultural land (Fairbanks et al., 2004; Rouget et al., 2003). Landscape fragmentation, along with intensive agricultural practices, are two aspects of agriculture that significantly influence biodiversity (Kehinde and Samways, 2012). However, agricultural landscapes within the CFR have much unprotected natural and semi-natural habitat with high conservation potential. Although farmland in the CFR and other Mediterranean areas are less impacted than in many other highly transformed regions (Cox and Underwood, 2011; Tilman et al., 2001), many critical habitats have been lost, and untransformed habitats are still threatened by future vineyard expansion (Fairbanks et al., 2004).

As parasitoids are functionally so important in agricultural mosaics, more information is required on how they respond to particular types of agricultural land-use, landscape structure, and other significant environmental factors. Parasitoids are highly diverse, with many species yet to be described (Bonet, 2009). Various species occupy a range of habitats and respond differently to environmental changes (Shaw, 2006). It is therefore important to understand how the agricultural mosaic maintains parasitoid diversity. In this chapter, I initially determine whether parasitoid species richness and assemblage structure differs among various biotope types within the agricultural mosaic. I also investigate which environmental variables are driving these differences relative to biotope type. This will promote understanding of the value of agricultural heterogeneity in these farmlands, and help to prioritise different types of patches for conservation in these landscapes. By understanding the environmental drivers for parasitoid diversity, we can better plan farmlands for their long-term maintenance.

## 2.2 Methods

### *2.2.1 Study area and design*

Sampling took place on 12 wine farms within the Cape Floristic Region (CFR) (Table 2.1, Fig. 2.1). The CFR of South Africa experiences a Mediterranean climate, with cold wet winters and warm dry summers. Parasitoids were collected during three seasons in 2015 and 2016: Autumn 2015 (May-June), late Spring 2015 (October-November), and mid-Summer 2016 (January-February). Samples were taken from five biotope types that dominate farmland mosaics in these winelands: 'vineyard', 'natural', 'old fields', 'riparian' and 'invaded' (Fig. 2.2). Vineyards are actively productive units, and followed the recommendations of the Biodiversity and Wine Initiative (2011). Detailed and up to date information about pesticide use in South Africa can be found at www.agri-intel.com. Natural habitats consisted of Boland granite fynbos, Swartland granite renosterveld and Swartland shale renosterveld. Old field sites are old vineyards abandoned due to lack of economic benefit for farmers. These sites were comprised mostly of weeds and grasses, with fynbos and renosterveld vegetation beginning to re-establish. Riparian sites consisted of a mixture of indigenous and alien vegetation, such as eucalyptus (*Eucalyptus* spp.) and acacia (*Acacia* spp.) trees, occurring alongside rivers. Invaded sites consisted of stands of invasive pine (*Pinus* spp.) and eucalyptus (*Eucalyptus* spp.) trees with sparse undergrowth.


Figure 2.1: Location of the wine farms used in the study, along with the four nearest towns.

Parasitoids were sampled from eight sites per biotope type, making a total of 40 sites. Sampling took place a minimum of 20 m from the biotope edge to avoid edge effects. Where more than one site occurred on a farm, sites of the same biotope were at least 500 m apart.

Table 2.1: Site locations with respective GPS coordinates and the number of sites per biotope type selected on each farm.

| Farm | Location (GPS Coordinates) | Number of sites | | | | |
|---|---|---|---|---|---|---|
| | | Vineyard | Natural | Old field | Riparian | Invaded |
| Babylonstoren | 33° 49'S, 18° 55'E | | | | 2 | |
| Bartinney | 33° 55'S, 18° 55'E | 2 | | | | |
| Bergsig | 33° 95'S, 18° 91'E | 1 | 1 | | 1 | |
| Delheim | 33° 52'S, 18° 53'E | | | | | 3 |
| Delvera | 33° 83'S, 18° 86'E | | 1 | 1 | | |
| Haut Espoir | 33° 56'S, 19° 06'E | | 1 | | 1 | |
| Knorhoek | 33° 52'S, 18° 52'E | 1 | | 1 | 1 | |
| Koopmanskloof | 33° 90'S, 18° 76'E | | 2 | 1 | | 1 |
| Lourensford | 34° 04'S, 18° 53'E | | | 2 | 3 | 3 |
| Mooiplaas | 33° 93'S, 18° 75'E | | 2 | 1 | | |
| Paul Cluver | 34° 10'S, 19° 06'E | 2 | 1 | 2 | | 1 |
| Reyneke Wines | 33° 52'S, 18° 45'E | 2 | | | | |

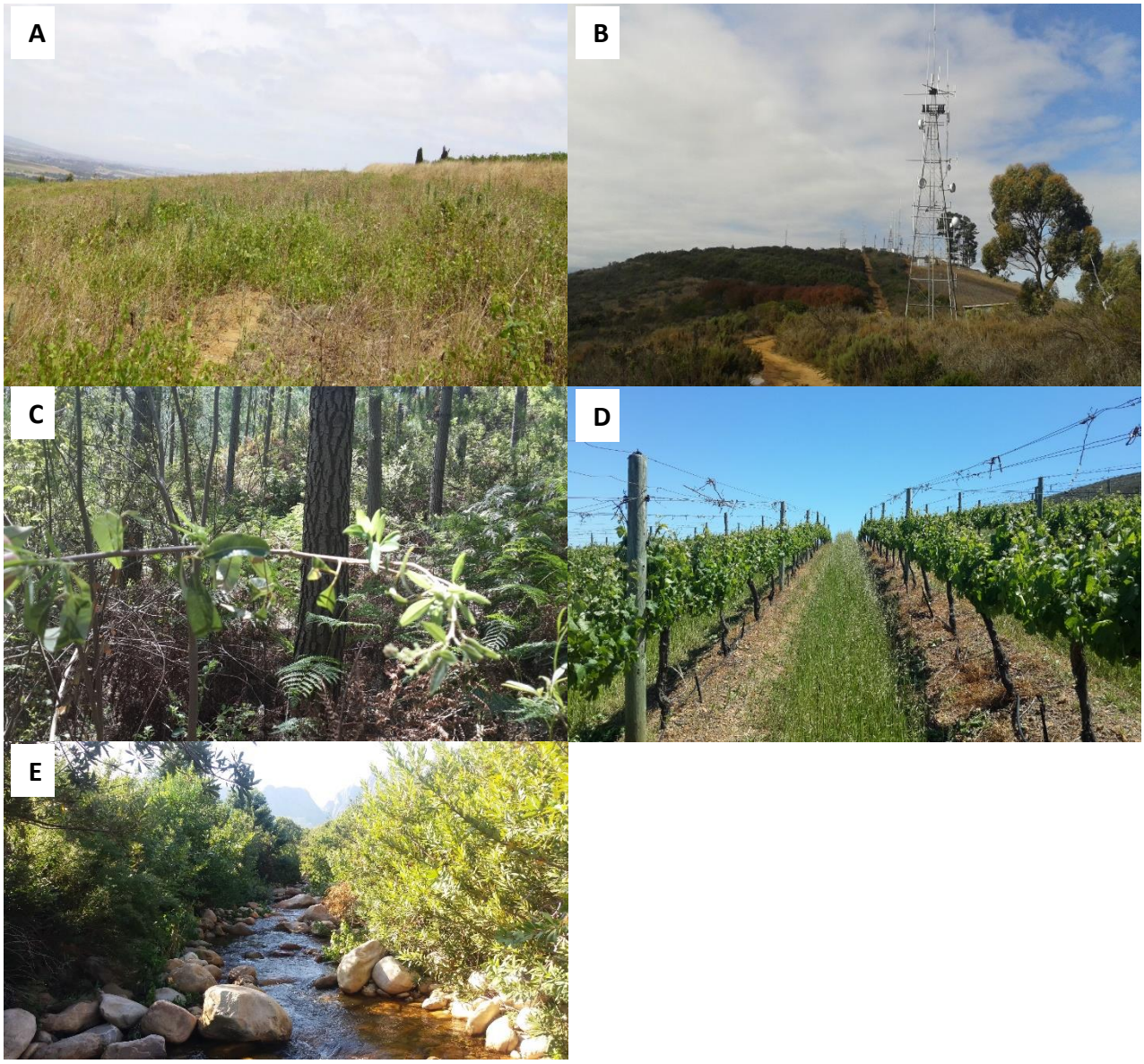


Figure 2.2: The various biotope sites that were sampled from. A) old field site on Delvera; B) natural site on Mooiplaas; C) invaded site on Delheim; D) vineyard site on Paul Cluver, and E) riparian site on Lourensford.

### *2.2.2 Parasitoid sampling*

Parasitoids were collected using a fuel powered leaf blower (SH 86, Stihl, Cape Town, South Africa), adjusted to vacuum setting and fitted with a fine mesh bag in the 10 cm diameter nozzle. At each site, vegetation was sampled by means of 100 insertions of the nozzle into the vegetation. In vineyards, an equal number of insertions were made on the vines and cover crops. Sampling took place under warm (about 20°C), sunny (<5% cloud cover) and dry

weather conditions to ensure that the vegetation was dry for sample collection. Samples were placed in plastic storage bags, and kept at -10°C until laboratory processing.

During laboratory processing, parasitoids were identified to morphospecies (Oliver and Beattie, 1996), as well as identified to family level using the keys in Goulet and Huber (1993), Prinsloo and Eardley (2012) and Prinsloo (1980). Reference specimens are currently stored in 75% ethanol in the Stellenbosch University Entomology Museum.

### *2.2.3 Environmental variables*

Environmental variables were assessed during the second sampling season in October-November 2015. Elevation, slope, vegetation composition and structure were recorded at each site (see the detailed list of variables in Table 2.2). Site-scale variables were collected using a 1 x 1 meter quadrat, replicated four times at each sampling site. Slope was categorized by subjective visual assessments, and each site was classified as flat, flat/medium, medium, medium/steep, and steep. QGIS 2.16.3 (QGIS Development Team, 2009) was used to calculate percentage cover of each of the five biotope types within a 500 m buffer zone around each site. The percentage cover of each respective biotope type was used as a proxy for the amount of each biotope available in the surrounding landscape. Distances to nearest natural area and nearest dam (farm reservoir used for irrigation) were also calculated using QGIS.

Table 2.2: Mean values of site and landscape-scale environmental variables per biotope type. Site-scale variables were recorded using a 1x1 meter quadrant replicated 4 times at each site. Landscape-scale variables were calculated using QGIS. Variables in bold were included in the model for statistical analyses. [1]

| Variables | Vineyard | | Natural | | Old Field | | Riparian | | Invaded | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | S.E. | Mean | S.E. | Mean | S.E. | Mean | S.E. | Mean | S.E. |
| Site-scale Variables | | | | | | | | | | |
| **average plant height (cm)** | **135.16** | **11.63** | **60.00** | **7.83** | **50.00** | **11.03** | **190.00** | **77.26** | **550.94** | **97.72** |
| **% plant cover** | **41.41** | **3.12** | **52.03** | **4.66** | **63.88** | **8.90** | **62.19** | **4.76** | **42.97** | **2.24** |
| % litter cover | 43.09 | 6.08 | 18.16 | 3.16 | 7.59 | 1.72 | 23.25 | 5.03 | 54.53 | 2.78 |
| **% bare ground** | **16.91** | **5.30** | **30.75** | **4.54** | **28.53** | **7.69** | **14.56** | **4.82** | **2.50** | **0.84** |
| **# flowering species** | **0.88** | **0.31** | **1.06** | **0.35** | **1.19** | **0.23** | **0.22** | **0.10** | **0.13** | **0.09** |
| # flowers | 8.22 | 3.97 | 15.34 | 5.54 | 10.16 | 2.77 | 8.59 | 5.85 | 1.19 | 1.15 |
| **# growth forms** | **4.38** | **0.56** | **3.38** | **0.26** | **2.75** | **0.25** | **3.88** | **0.44** | **2.38** | **0.46** |
| **% veg naturalness[2]** | **11.98** | **2.76** | **50.53** | **4.74** | **41.44** | **9.70** | **44.88** | **9.79** | **9.19** | **3.70** |
| **Plant species richness** | **4.44** | **0.70** | **5.16** | **0.50** | **4.03** | **0.40** | **3.75** | **0.17** | **3.09** | **0.46** |
| % weed cover | 7.33 | 2.04 | 0.31 | 0.17 | 21.11 | 6.12 | 2.47 | 0.89 | 0.41 | 0.41 |
| % alien cover | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 14.84 | 7.82 | 32.50 | 4.01 |
| % tree cover | 0.00 | 0.00 | 0.94 | 0.66 | 0.00 | 0.00 | 3.75 | 2.83 | 0.00 | 0.00 |
| % shrub cover | 0.47 | 0.25 | 34.78 | 4.44 | 1.59 | 1.46 | 25.44 | 10.46 | 4.59 | 2.96 |

[1] Slope was not included in the table as it was recorded as a categorical variable, but was included in all models.
[2] Percentage native species per quadrat

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| % restio[3] cover | 0.00 | 0.00 | 1.91 | 1.09 | 2.03 | 2.03 | 4.22 | 1.86 | 0.00 | 0.00 |
| % grass cover | 10.70 | 2.40 | 10.75 | 1.06 | 35.00 | 9.92 | 11.03 | 3.06 | 3.03 | 1.17 |
| % herbs & forbs cover | 0.81 | 0.47 | 2.16 | 1.36 | 2.81 | 2.81 | 0.44 | 0.44 | 1.56 | 1.05 |
| % agricultural weed cover | 19.31 | 3.84 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| % vine cover | 22.09 | 2.06 | 0.00 | 0.00 | 1.33 | 0.89 | 0.00 | 0.00 | 0.88 | 0.88 |
| Landscape-scale Variables | | | | | | | | | | |
| **Elevation (m)** | **324.88** | **45.30** | **338.50** | **38.81** | **314.88** | **28.57** | **251.50** | **35.05** | **348.88** | **40.99** |
| Distance to nearest dam (m) | 416.72 | 72.90 | 615.05 | 199.94 | 623.46 | 158.48 | 1045.29 | 309.43 | 867.88 | 251.94 |
| **Distance to nearest natural area (m)** | **952.15** | **335.74** | **0.00** | **0.00** | **424.42** | **94.33** | **541.49** | **188.54** | **780.35** | **183.21** |
| **% Natural area** | **5.46** | **3.26** | **63.14** | **4.91** | **16.00** | **7.43** | **20.91** | **9.77** | **9.35** | **7.42** |
| **% Vineyard area** | **64.48** | **11.31** | **28.86** | **5.26** | **37.69** | **9.27** | **55.33** | **9.03** | **18.45** | **5.23** |
| **% Old Field area** | **11.58** | **5.60** | **2.10** | **0.95** | **25.08** | **3.97** | **3.25** | **1.03** | **15.66** | **4.06** |
| **% Riparian area** | **4.56** | **4.44** | **4.36** | **2.91** | **0.00** | **0.00** | **19.45** | **3.73** | **0.00** | **0.00** |
| **% Invaded area** | **13.91** | **12.02** | **1.54** | **1.43** | **21.24** | **6.28** | **1.06** | **1.06** | **56.54** | **8.16** |
| **% Biotope size** | **64.48** | **11.31** | **63.14** | **4.91** | **25.08** | **3.97** | **19.45** | **3.73** | **56.54** | **8.16** |
| **# Biotopes** | **2.75** | **0.31** | **3.25** | **0.16** | **3.50** | **0.19** | **3.38** | **0.26** | **3.13** | **0.35** |

[3] 'restio' = native vegetation in the family Restionaceae

### *2.2.4 Data analyses*

Parasitoid data for all three seasons were pooled. Primer 6 (PRIMER-E, 2008) was used to perform a Permutational multivariate analysis of variance (PERMANOVA) to test for differences in parasitoid assemblages between the various biotope types. Biotope type was included as a fixed variable. A random variable was included, namely GenLoc, representing the general location within which each farm occurred. GenLoc included the areas Elgin (34.15°S, 19.00°E), Stellenbosch (33.93°S, 18.86°E), Somerset West (34.08°S, 18.84°E) and Franschhoek (33.89°S, 19.15°E) (Fig. 2.1). The random variable was used to account for the unequal distribution of sites among locations and spatial autocorrelation effects. A visualization of differences in parasitoid assemblage structure between biotope types was created by performing a canonical analysis of principal coordinates (CAP) in Primer 6 (PRIMER-E, 2008). CAP and PERMANOVA analyses were both based on Bray-Curtis similarities derived from square-root transformed abundance data. Pseudo-F statistics and P-values were estimated using 999 permutations.

Before testing for the effect of environmental variables on patterns in parasitoid assemblage structure, Spearman rank order correlations were carried out using Statistica 12 (2003) to determine which environmental variables significantly correlated with one another. Correlations with an R-value greater than 0.6 resulted in one of the environmental variables being excluded from the model. A BIO-ENV analysis (biota and/or environmental matching) was then performed in Primer 6 (PRIMER-E, 2008) to test whether environmental variables influence parasitoid assemblage structures. BIO-ENV analyses select the abiotic variable subset that maximises rank correlation between biotic and abiotic similarity matrices (Clarke and Warwick, 2001). The BIO-ENV analysis was based on a Euclidean distance matrix derived from log(x+1) transformed and normalised environmental data. To obtain values for the amount of variation that these environmental variables explain, a distance based linear model (DistLM) was carried out in Primer 6 (PRIMER-E, 2008). A forward selection procedure was used to identify the best combination of variables that explained variation in parasitoid assemblage patterns. Akaike's Information Criterion (AIC) was used as the selection criterion (Anderson et al., 2008; Johnson and Omland, 2004). Pseudo-F statistics and P-values were estimated using 999 permutations.

Generalized linear models were performed in Statistica 12 (2003) to investigate the influence of biotope type and the environmental variables highlighted in bold in Table 2.2 on parasitoid species richness and family richness. Shapiro-Wilks tests (Statistica 12, 2003) were carried out to test for normality of distribution of parasitoid species richness and family richness. Based on the Shapiro-Wilks test for parasitoid species richness, Poisson distribution and log-link function was used (Bolker et al., 2009). Normal distribution was used for parasitoid family richness. To select the best variables explaining variation in the model, backwards stepwise selection was used. Model selection criteria was based on AIC (Johnson and Omland, 2004). For significant categorical variables, Tukey HSD and LSD comparisons were carried out in Statistica 12 (2003).

## 2.3 Results

### *2.3.1 Effect of biotope and environmental variables on assemblage structure*

A total of 1817 parasitoids were sampled in 351 morphospecies, 22 families and 7 super families. The most species-rich families were Eulophidae, Platygastridae and Braconidae. Eulophidae was most dominant in natural, semi-natural and invaded biotopes. Braconidae dominated riparian habitats and Platygastridae was the most dominant family in vineyards (Appendix D).

Parasitoid families are well represented in each biotope. The dominant families, and a large portion of the other families, were recorded in all biotopes (Fig.2.4). Of the 23 families, 96% occurred in riparian habitats, 78% were found in both natural and invaded habitats, while 74% and 65% occurred in old fields and vineyards respectively.

The CAP ordination shows high dissimilarity in parasitoid assemblage structure between the five biotope types (Fig.2.3). This is further supported by PERMANOVA results (Pseudo-F=1.896, P=0.001) indicating significant differences in parasitoid assemblage structure among biotope types. Post-hoc comparisons show parasitoid assemblages differ significantly between each biotope type (Table 2.3).

The less disturbed sites (natural, old fields and riparian sites) shared the highest number of species (Table 2.4). High proportions of parasitoid species were sampled from riparian (51%) and natural (37%) vegetation, and were unique to those biotope types (Table 2.4). The more

disturbed old field, invaded and vineyard biotopes had lower proportions of unique species (29%, 27% and 22% respectively).

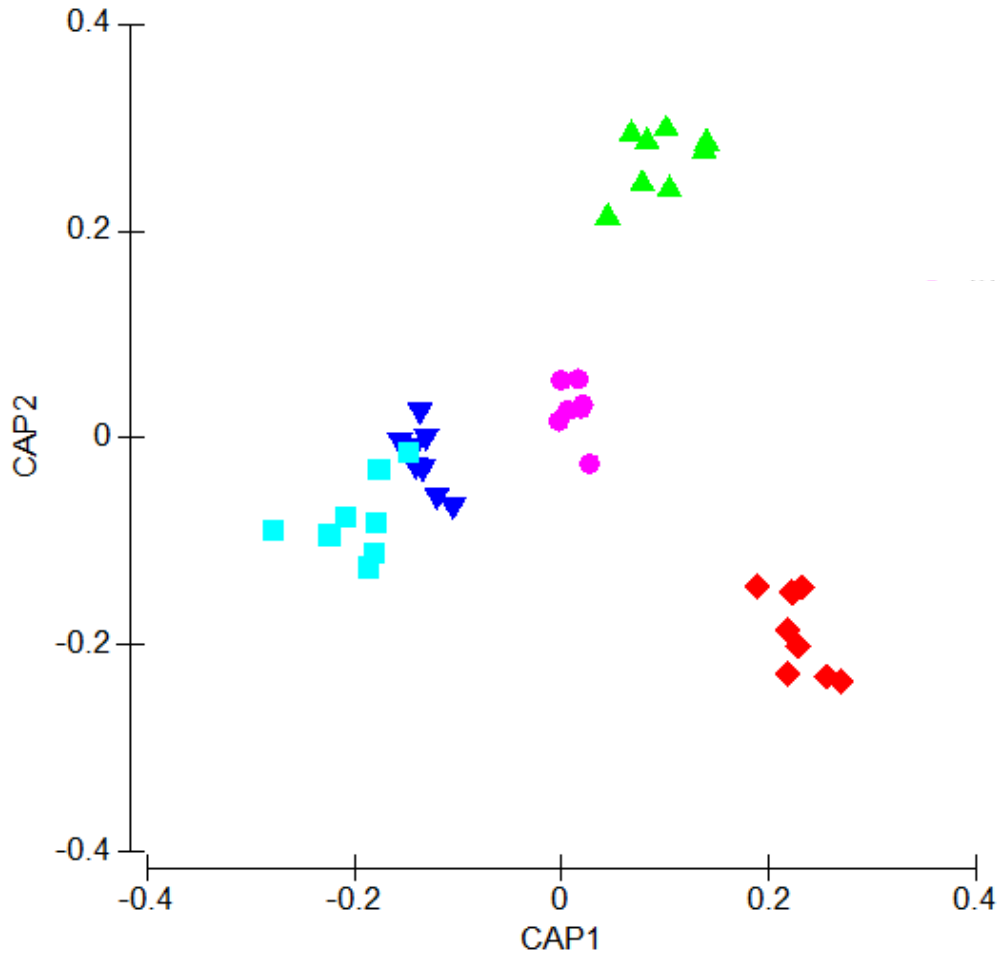


Figure 2.3: Ordination of CAP analysis indicating differences in parasitoid assemblage structure between each biotope type. Based on Bray-Curtis similarities and derived from square root transformed parasitoid abundance data. Green triangle= vineyard, blue triangle = natural, cyan square= old field, red diamond = riparian, purple circle = invaded.

Table 2.3: t-values derived from PERMANOVA analysis with their respective levels of significant difference between each biotope type.

| | **Vineyard** | **Natural** | **Old field** | **Riparian** |
|---|---|---|---|---|
| **Natural** | 1.6808** | | | |
| **Old field** | 1.2702** | 1.4632** | | |
| **Riparian** | 1.3005** | 1.5644** | 1.4674** | |
| **Invaded** | 1.2107* | 1.2809* | 1.1887* | 1.3193** |

*P<0.05, **P<0.005, ***P<0.001

Table 2.4: Number of parasitoid species shared between each biotope type as well as the proportion of parasitoid species that are unique to that biotope type. Percentage values represent proportion of total parasitoid species that are shared between the two biotope types being compared.

| | | Vineyard | Natural | Old field | Riparian | Invaded |
|---|---|---|---|---|---|---|
| **Shared species** | Natural | 27 (5%) | | | | |
| | Old field | 35 (7%) | 56 (13%) | | | |
| | Riparian | 42 (9%) | 46 (10%) | 48 (11%) | | |
| | Invaded | 19 (3%) | 37 (8%) | 27 (5%) | 34 (7%) | |
| **Unique species** | Number of unique species | 16 | 49 | 34 | 91 | 21 |
| | Total species | 72 | 134 | 116 | 177 | 77 |
| | Proportion unique (%) | 22.2 | 36.6 | 29.3 | 51.4 | 27.3 |

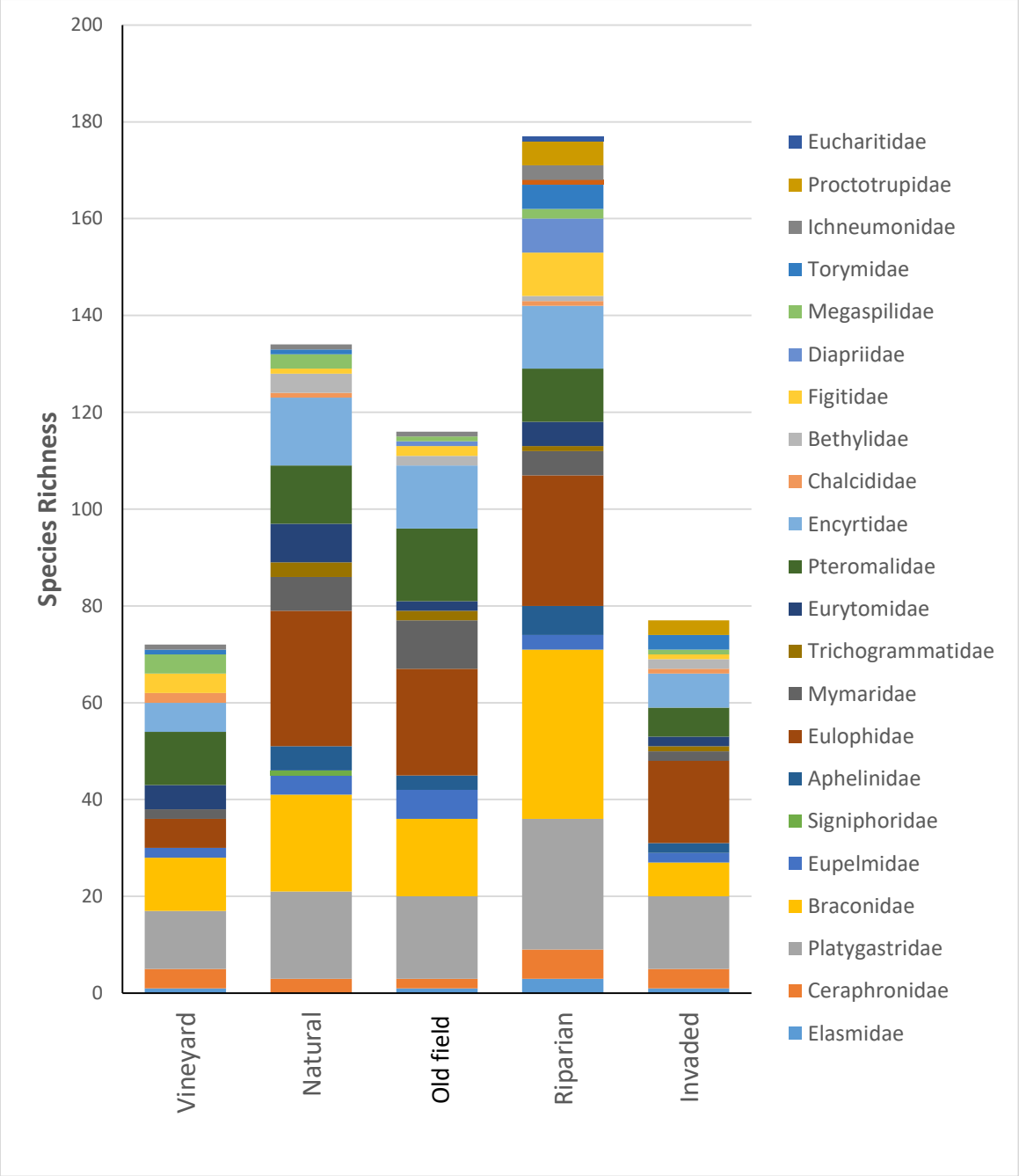


Figure 2.4: Mean parasitoid species richness within families in each biotope type. Colours represent various parasitoid families and their contribution to total species richness at each biotope type.

Based on results from Spearman rank order correlations, 16 of the 28 environmental variables recorded were used in the BIO-ENV model (Table 2.2). According to the BIO-ENV analysis, five environmental variables significantly influenced parasitoid assemblage structure ($P<0.01$, Correlation value = 0.316). The significant environmental variables are as follows: average

plant height, percentage bare ground, percentage natural vegetation, slope, and percentage riparian area. DistLM sequential tests further supported these results by showing that the above-mentioned environmental variables all influenced parasitoid assemblage structure (Table 2.5), and together explained 10.38% of total variation in assemblage structure.

Table 2.5: Results from distance-based linear model analysis, showing respective Pseudo-F statistics and P-values of environmental variables that significantly influenced parasitoid assemblage structure using a BIO-ENV analysis.

| Variables | Pseudo-F | P-value |
|---|---|---|
| Average plant height | 1.50 | 0.012 |
| % Bare ground | 1.48 | 0.010 |
| % Natural vegetation | 1.65 | 0.004 |
| Slope | 1.79 | 0.002 |
| % Riparian area | 1.83 | 0.001 |

### *2.3.2 Effect of biotope and environmental variables on species and family richness*

Generalized linear models revealed that biotope type significantly influenced parasitoid species and family richness (Table 2.6, Fig. 2.5). Tukey HSD and LSD analyses revealed significant differences between biotopes for parasitoid species and family richness (Fig. 2.5, A and B). For parasitoid species and family richness (Fig. 2.5, A and B), riparian habitats differ significantly from the highly disturbed vineyard and invaded biotopes, with higher mean values for both species and family richness. Richness in old fields was intermediate between natural and disturbed biotopes (Fig. 2.5, A). There were positive relationships between percentage natural area in the surrounding landscape and in both species and family richness (Table 2.6, Appendix A, Appendix C). There was a positive relationship between the number of plant growth forms and parasitoid family richness (Table 2.6, Appendix B).

Table 2.6: Results from generalized linear models with significant environmental variables for parasitoid species richness and family richness. Wald-statistics, P-values and the nature of the relationship between variables are given.

| | Wald-Statistic ($\chi^2$) | P-value | Relationship |
|---|---|---|---|
| **Species Richness** | | | |
| Average plant height | 5.66 | 0.017 | Negative |
| % Biotope size | 4.12 | 0.042 | Negative |
| % Vineyard area | 16.88 | <0.001 | Negative |
| % Natural area | 5.64 | 0.018 | Positive |
| Biotope type | 57.62 | <0.001 | |
| General location | 17.29 | 0.001 | |
| Slope | 21.56 | <0.001 | |
| **Family Richness** | | | |
| Average plant height | 8.08 | 0.005 | Negative |
| Number of growth forms | 4.09 | 0.043 | Positive |
| % Bare ground | 14.53 | <0.001 | Positive |
| Number of flowering species | 8.44 | 0.004 | Positive |
| % Natural area | 11.79 | 0.001 | Positive |
| % Vineyard area | 14.13 | <0.001 | Positive |
| % Natural vegetation | 5.15 | 0.023 | Positive |
| General location | 24.75 | <0.001 | |
| Biotope type | 65.16 | <0.001 | |
| Slope | 24.28 | <0.001 | |

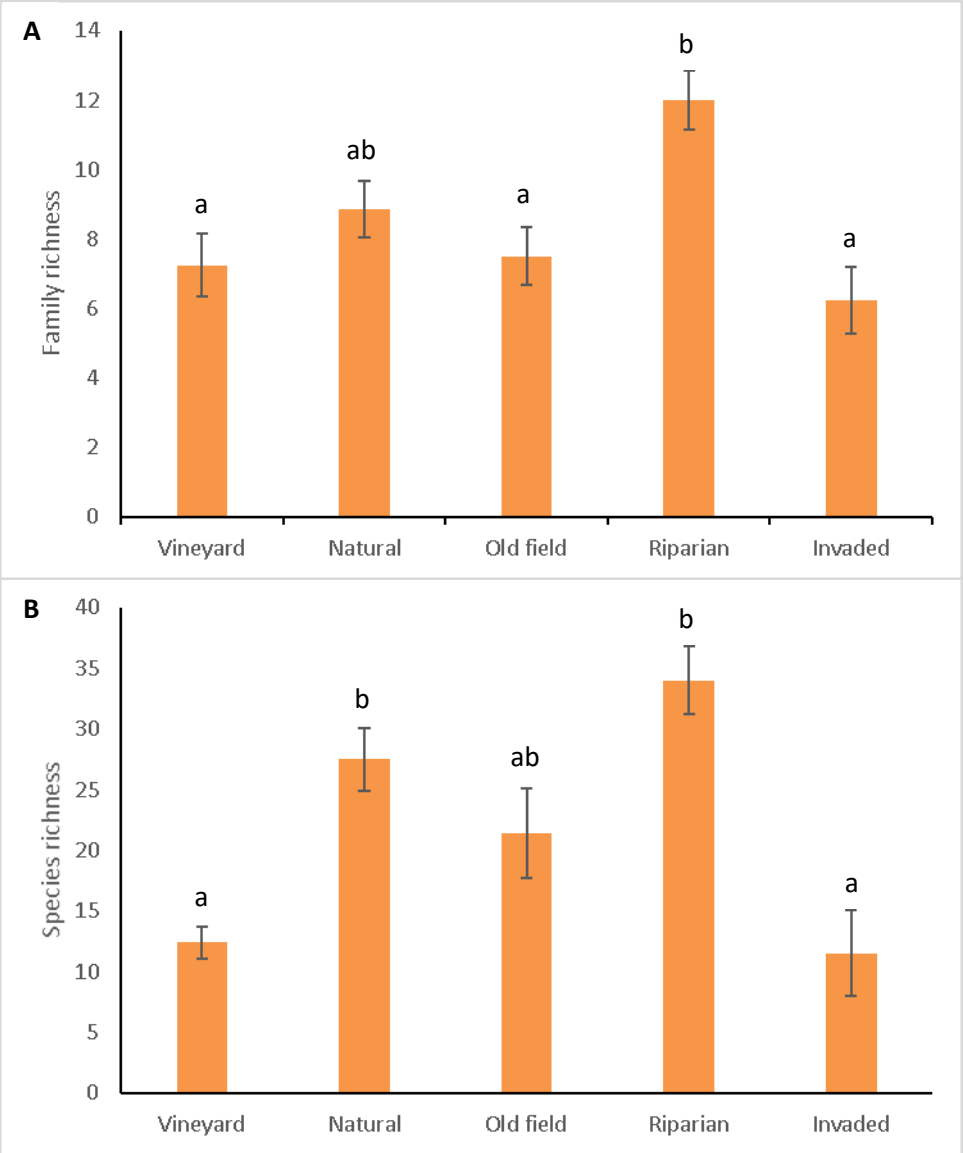


Figure 2.5: Mean parasitoid A) family richness and B) species richness at each of the five biotope types, with standard errors. Biotopes with letters in common are not significantly different from one another at $P < 0.05$.

## 2.4 Discussion

### *2.4.1 Biodiversity value of the five biotope types*

Parasitoid assemblage structure differs greatly among various biotope types, with the less disturbed riparian and natural biotopes showing highest parasitoid species richness and highest percentage of unique species. This is in accordance with the findings of Vrdoljak and Samways (2013) on flower-visiting insects, and illustrating the high value of remnant habitats for maintaining insect diversity. They also stressed that natural, near natural and even transformed habitats make large contributions to total diversity. Furthermore, the abundance of various beneficial natural enemies, including parasitoids, was higher in vineyards adjacent to undisturbed, wooded vegetation, as found by Thomson and Hoffmann (2009) in Australian landscapes. Species-rich riparian habitats have also previously been found to increase predator abundance and colonization of nearby vineyards in northern California (Nicholls et al., 2001). These findings emphasize the value of preserving natural and near-natural remnants within agricultural landscapes as refuges for natural enemies.

Parasitoid species richness within old fields here was lower than the undisturbed natural and riparian habitats, but higher than vineyards and invaded habitats. Old fields are known to support diverse arthropod assemblages within CFR agricultural mosaics (Gaigher et al., 2016), making them important habitat elements for farmland biodiversity. Although old fields are previously disturbed biotopes, and not as speciose as natural and riparian habitats, they may hold great potential as stepping-stones between highly disturbed and undisturbed habitats, assisting with the movement and connectivity of insect populations within agricultural landscapes, as in the case of flower-visitors (Vrdoljak and Samways, 2013). Here, old fields shared the highest percentages of parasitoid species with natural and riparian habitats, which emphasizes the biodiversity value of fallow land.

Invaded and vineyard biotopes had markedly lower parasitoid species richness than the other three biotopes. For invaded biotopes, this is in accordance with the findings of Magoba and Samways (2012) on epigaeic arthropods, where species richness in areas invaded by alien trees was very low. However, they also found that vineyards had higher epigaeic arthropod species richness than in invaded areas, which is not the case here for parasitoids in these vineyards, although alien-invaded biotopes were species-poor in parasitoids. These findings

agree with Mlambo et al. (2011) who found that monotypic biotopes, such as vineyards and sites invaded by alien trees, had far lower species abundance than botanically diverse biotopes.

### *2.4.2 Significant environmental variables for assemblages*

Percentage natural vegetation and percentage riparian area in the surrounding landscape influenced parasitoid assemblage structure, stressing further the importance of natural remnants. Additionally I found that percentage natural area positively correlated with both parasitoid species and family richness. Natural habitats are therefore essential for the maintenance of parasitoid diversity within farmland mosaics. This may be due to the high levels of plant species richness (supporting many host insects), and ultimately the great habitat complexity in this biotope. This is especially relevant in the CFR, with its high levels of botanical diversity.

Floral nectar is a critical component of adult parasitoid diets (Landis et al., 2000). The high floral diversity in the fynbos may represent an important resource for parasitoids, which was supported here by the number of flowering species correlating positively with a number of parasitoid families. I also found that parasitoid family richness increased with number of plant growth forms, suggesting that structurally complex habitats may sustain more complex and functionally diverse parasitoid assemblages. This is consistent with studies that have shown that plant diversity and complexity increases parasitoid diversity (Fraser et al., 2007; Pak et al., 2015). Furthermore, late successional plant assemblages that are common in less disturbed habitats are probably crucial for the maintenance of diverse parasitoid assemblages, with these plant assemblages providing essential resources that are otherwise scarce in agricultural habitats (Marino et al., 2006).

### *2.4.3 Composition of families across the different biotope types*

Here, species richness within dominant parasitoid families were similar across all biotope types, and most families were recorded in all biotope types. The different families represent a wide range of functional guilds specialising on hosts from widely different taxa (Prinsloo and Eardley, 2012). The occurrence of similar patterns of parasitoid families among biotopes suggests that although vineyard and invaded habitats are home to far fewer parasitoid species, they may still maintain functionally diverse assemblages of parasitoids, but just in

lower species numbers. Although species richness provides valuable insight into differences between biotopes, it does not signify ecological function. A biotope may be more affected by loss of specific functionally important species than by loss of species in general (Vrdoljak and Samways, 2013).

High species richness within families may nevertheless contribute to greater ecological resilience in less disturbed biotopes. By maintaining a high species diversity within functional groups, species are able to recover from disturbances more easily due to a high number of insurance species that may become important as soon as other species disappear (Bengtsson et al., 2003). This is especially important in agricultural landscapes where local extinction is a regular occurrence (Tscharntke et al., 2005). The ecological resilience of habitats to disturbance can come about by preserving a high diversity of seemingly redundant species (Bengtsson et al., 2003). These seemingly redundant species may become important for the biological control of pests after disturbance (Ives and Cardinale, 2004).

### *2.4.4 Conservation implications*

Within the CFR, there is high potential for agricultural expansion especially as there is also much natural habitat still in existence outside the local protected areas. Previous studies have emphasized the potential of, and need for, conservation of privately owned remnant habitats within Mediterranean agricultural systems (Cox and Underwood, 2011; Viers et al., 2013). A vinecology approach, as suggested by Viers et al. (2013), whereby ecology and viticultural practices are integrated may be the answer to the fundamental issue of balancing agricultural success with biodiversity conservation. Farming practices within agricultural landscapes must take into account their impact on both biodiversity and ecosystem services provided by remnant habitats. Through a diversity of habitats across the landscape, diverse assemblages of agriculturally important insects can be maintained, as shown here for these diverse parasitoid assemblages. The five biotopes here had different parasitoid assemblage structures, suggesting that each biotope makes a unique contribution to overall biodiversity, ultimately increasing heterogeneity across the agricultural landscape. This means that it is essential for conservation efforts within agricultural landscapes to maintain habitat heterogeneity to preserve the high diversity of parasitoid species and families across the landscape.

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# Chapter 3

## Spatiotemporal change of parasitoid wasp assemblages across agricultural mosaics within the Cape Floristic Region, South Africa

**Abstract**

Agricultural landscapes experience various seasonal disturbances and inputs, exposing arthropod populations to temporal fluctuations in resource availability. Various arthropod natural enemies, including parasitoid wasps, are required to move across agricultural mosaics in search of resources and refuge habitats during times of stress. Few studies have considered the temporal variability of habitat patches across farmland mosaics, especially within the Cape Floristic Region, South Africa. To investigate the distribution of parasitoids seasonally, I assessed the change of parasitoid diversity and assemblage structure across different dominant biotope types within farmland mosaics over three seasons. These biotopes were vineyards, old fields, riparian vegetation, remnant natural vegetation and areas invaded by alien trees. Sample seasons were autumn, spring and summer. Parasitoid assemblage structure differed between the various biotope types and across all seasons, suggesting that there is both spatial and temporal turnover of species across the various landscape elements in response to seasonal changes and their associated environmental conditions. It is clear that a landscape perspective is necessary for the protection of these beneficial natural predators, in particular habitat heterogeneity and patch isolation are important factors that need to be taken into consideration when promoting species turnover across agricultural landscapes. By investigating the influence of spatiotemporal variability of agricultural landscapes on arthropods, farm managers may plan human-induced disturbances more accurately to conserve predator assemblages and ultimately preserve natural biological control within farmland mosaics.

## 3.1 Introduction

Agricultural landscapes experience various human-induced influences, such as the use of chemical pesticides and fertilisers, fragmentation of natural vegetation, degradation and simplification of habitats, and the spread of invasive alien plants and animals (Burel et al., 2004; Schroth et al., 2004). Some of these disturbances are seasonal in nature, such as when crop fields undergo sowing and harvesting, insects are exposed to temporal fluctuations in resource availability. Remnant natural patches are essential habitats for native species, serving as refuges during these times of disturbance (Phalan et al., 2011). Non-crop habitats are thus more stable and diverse environments over time (Bianchi et al., 2006). These habitats also become important during the cold-wet winter months in the Cape Floristic Region (CFR), South Africa, when vineyards lose their leaves. A diversity of habitat types within agricultural landscapes is therefore crucial for the provision of a range of important resources for various arthropods, including hymenopteran parasitoids (Cronin and Reeve, 2005).

Arthropods utilize various habitat types and obtain resources from a variety of habitat patches across the landscape (Bianchi et al., 2006). Heterogeneous mosaics increase functional connectivity within farmlands which is important for arthropod survival within fragmented agricultural landscapes (Gaigher et al., 2016). Although some species are confined to natural or near-natural habitats, many others utilize disturbed areas such as crops and tree plantations (Daily et al., 2003; Eilu et al., 2003). It is thus necessary to manage various landscape elements to conserve a wide range of species (Bennett et al., 2006). Tscharntke et al. (2005) stressed the importance of acknowledging population interactions between areas of varying disturbance regimes, as well as various land-use intensities. Some species require multiple populations in various suitable habitats and successful movement between these habitats to ensure survival (Opdam, 1991). For other species, it is necessary to move across different biotopes in search of resources to satisfy daily or seasonal needs (Law and Dickman, 1998).

It is widely established that habitat fragmentation is detrimental towards natural enemies, including parasitoids, reducing both biodiversity and parasitism (Kruess and Tscharntke, 1994). This may result in pest outbreaks as pest insects are released from parasitism. Functionally important arthropods, including parasitoids, are thus required to maintain the resilience of ecosystem processes such as the control of insect pests (Walker, 1992). Within

agroecosystems, fragmentation of natural habitats is expected and the isolation of small populations surrounded by disturbed habitats is thus unavoidable. Agricultural landscapes designed to preserve connectivity between habitats may aid with the biological control of pests (Kruess and Tscharntke, 1994).

Movement across fragmented agricultural landscapes is essential for the survival of plant and animal species (Wiens et al., 1993). Many arthropods use different habitat elements for various stages of their life-cycle. For example, some predatory beetles reproduce in arable fields and utilize field margins for hibernation (Holland, 2002). Various linyphiid spiders disperse into natural habitats following harvest and use arable fields for hibernation (Thorbek et al., 2004). Increased connectivity between habitats within agricultural mosaics is vital for arthropod dispersal, as was shown by Maisonhaute and Lucas (2010) regarding the distribution of predatory beetles between crop fields and field margins. The ease at which species are able to move between habitat types is largely dependent on their mobility (Tscharntke et al., 2007). This is important for natural enemies such as parasitoids, as they are forced to obtain resources from non-crop habitats when vineyards become more hostile during times of harvest (Landis and Menalled, 1998).

Parasitoids are able to forage across wide ranges and will therefore be able to utilize a range of habitats to ensure their survival (Cronin and Reeve, 2005; Bianchi et al., 2006). These organisms operate at a high trophic level and have an inclination to be highly specialized, making them vulnerable to extinction (Shaw, 2006; Shaw and Hochberg, 2001). Their sensitivity towards changes in habitat conditions and resource availability highlights the importance of heterogeneous mosaics within agricultural landscapes. Habitat fragmentation and isolation within agricultural landscapes negatively impacts the perseverance of parasitoid populations (Kruess and Tscharntke, 2000), particularly specialist parasitoids as they are restricted to a narrower variety of prey resources and habitat types (Rand and Tscharntke, 2007).

While many studies have focussed on the spatial patterns of natural enemies across agricultural landscapes, few have considered the influence of temporal variability on these patterns, especially within the CFR. It is for this reason that I will examine how parasitoid diversity and assemblage structure differs over time within agricultural landscapes. Here, I compare parasitoid assemblages over three different seasons and across five biotope types.

I aim to investigate how parasitoid assemblages found at certain biotope types, change from one season to the next. This will allow me to gain insight into the importance of individual habitat types within the agricultural mosaic during various times of resource availability and environmental conditions for parasitoids. This will also allow me to determine the spatial and temporal turnover rates for the functionally important parasitoids in these agricultural landscapes.

## 3.2 Methods

### *3.2.1 Study area and design*

Parasitoids were sampled from 12 wine farms within the Cape Floristic Region (CFR), South Africa (Fig. 2.1). This area experiences a Mediterranean climate, with cold wet winters and warm dry summers. Samples were collected during the following 3 seasons in 2015 and 2016; Autumn 2015 (May-June), late Spring 2015 (October-November), and mid-Summer 2016 (January-February). During autumn the temperature begins to drop to approximately 20°C. Spring experiences warmer days, reaching an average of 25°C, and in the summer temperatures are often in the range of mid to high 30°C (Climate-Data.org, 2017).

Parasitoids were sampled from five biotope types that dominate agricultural mosaics in the winelands: 'vineyard', 'natural', 'old fields', 'riparian' and 'invaded'. Natural habitats are made up of Swartand shale renosterveld, Swartland granite renosterveld and Boland granite fynbos. Here, old vineyards that have been abandoned due to lack of economic benefit for farmers are classified as old field sites. Old field sites consisted mostly of grasses and weeds, with natural vegetation beginning to return. Riparian sites were comprised of a combination alien and indigenous vegetation found alongside rivers. Invasive pine (*Pinus* spp.) and eucalyptus (*Eucalyptus* spp.) trees with sparse undergrowth were characteristic of invaded sites.

Parasitoids were collected from a total of 40 sites, eight from each biotope type. In order to avoid edge effects, samples were collected at least 20 m from the biotope edge. Within one farm, sites of the same biotope type were a minimum of 500 m apart.

### *3.2.2 Parasitoid sampling*

A fuel powered leaf blower (SH 86, Stihl, Cape Town, South Africa) was used for parasitoid sampling. The leaf blower was adjusted to vacuum setting and fitted with a fine mesh bag in

the 10 cm diameter nozzle. The nozzle was inserted into the vegetation 100 times at each site. In vineyards, the vines and cover crops received an equal number of insertions. Other studies that used the vacuum sampling method include Gaigher et al., 2015 and 2016. Sampling took place under warm (about 20°C), sunny (<5% cloud cover) and dry weather conditions to ensure that the vegetation was dry for sample collection. Samples were kept at -10°C, in plastic storage bags, until laboratory processing.

Parasitoids were identified to morphospecies (Oliver and Beattie, 1996) during laboratory processing. The keys in Goulet and Huber (1993), Prinsloo and Eardley (2012) and Prinsloo (1980) were used to identify parasitoids to family level. Reference specimens are currently stored in the Stellenbosch Entomology Museum, in 75% ethanol.

### *3.2.3 Data Analyses*

Generalized linear models were carried out in Statistica 12. First order models were calculated to investigate the influence of biotope type and season on parasitoid abundance, species richness and family richness, then second order models were created, which are the same models as the first order, but additionally the interactions between biotope type and season were included (Bolker et al., 2009; Statistica 12, 2003). For parasitoid species richness and abundance, Poisson distribution and log-link function were used. Normal distribution and log-link function were used for parasitoid family richness. Primer 6 (PRIMER-E, 2008) was used to perform permutational multivariate analyses of variance (PERMANOVA) to test for differences in parasitoid assemblages between biotope types across the three seasons, as well as for possible interactions between biotope type and season (Anderson et al., 2008; Clarke and Warwick, 2001). A canonical analysis of principal coordinates (CAP) was performed in Primer 6 (PRIMER-E, 2008) to create visualisations of the differences in parasitoid assemblage structures between biotope types within seasons, as well as between seasons within biotopes. CAP and PERMANOVA analyses were both based on Bray-Curtis similarities derived from square root transformed abundance data. Pseudo-F statistics and P-values were estimated using 999 permutations.

## 3.3 Results

### *3.3.1 Effect of season and biotope on parasitoid richness and abundance*

Parasitoid species richness, abundance and family richness are all significantly influenced by season (Table 3.1), indicating variation in parasitoid numbers over time. Biotope type had a significant influence on parasitoid species richness, but not on abundance or family richness (Table 3.1). There were no significant season x biotope type interactions for any of the response variables (Table 3.1). Abundance and richness patterns were relatively constant among biotopes for all seasons. A similar trend can be seen for both parasitoid family and species richness for all biotope types across the three seasons (Fig. 3.1 A and C). However, parasitoid abundance exhibits somewhat different overall patterns across the biotope types for the different seasons (Fig. 3.1 B), with relatively greater parasitoid abundance in summer in old fields compared to the other seasons.

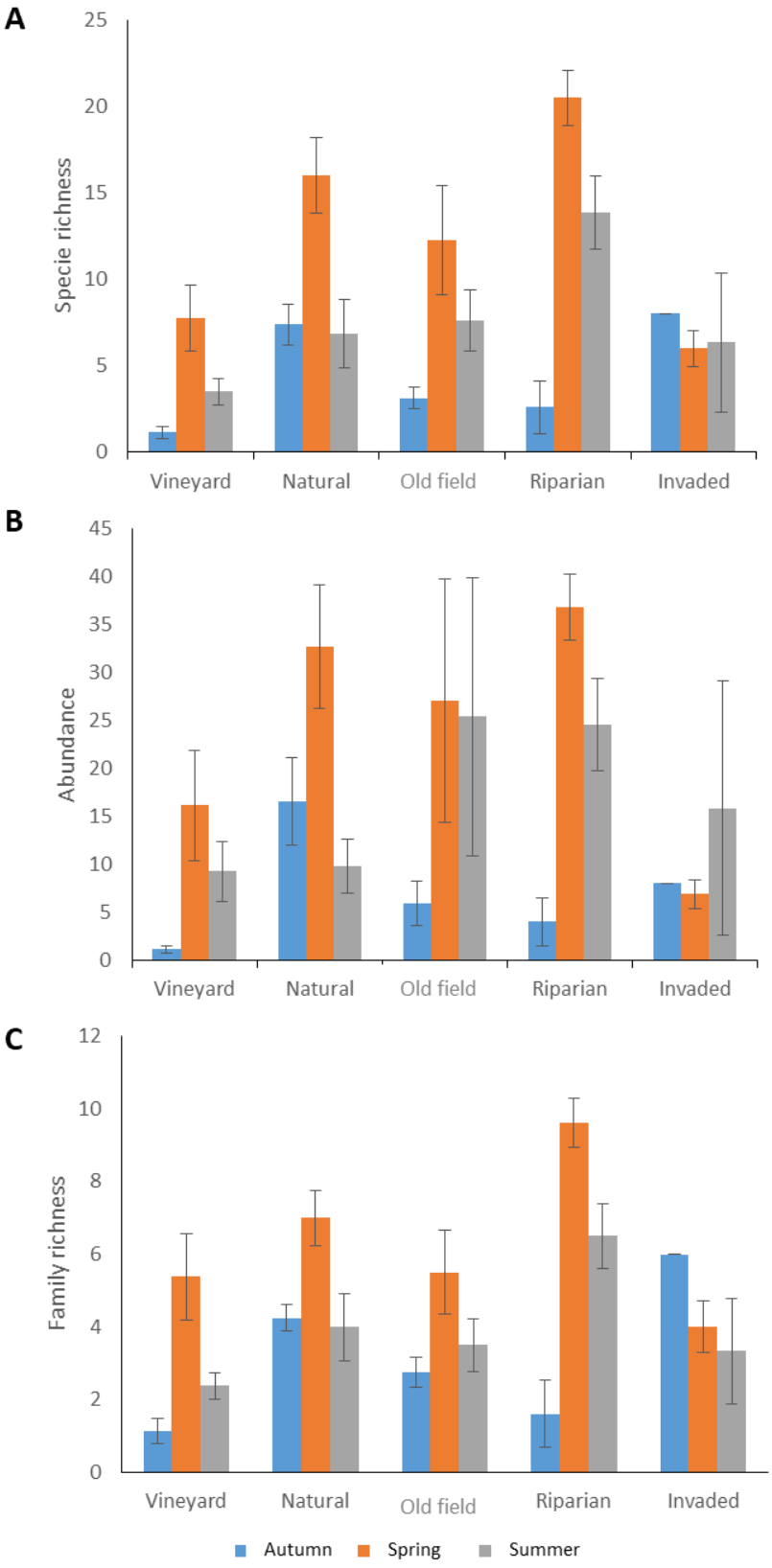


Figure 3.1: Mean parasitoid A) Species richness (number of species), B) Abundance (number of individuals) and C) Family richness (number of species) found at each biotope type for each of the three seasons, with standard errors.

Table 3.1: Results from generalized linear models for relationships between season, biotope type and the season x biotope type interaction for parasitoid species richness, abundance and family richness. Wald-statistics and p-values are displayed.

| | Wald Statistic | p-value |
|---|---|---|
| **Species richness** | | |
| Season | 29.25 | <0.001 |
| Biotope type | 17.77 | 0.001 |
| Season x biotope type interaction | 15.24 | 0.055 |
| **Abundance** | | |
| Season | 7.88 | 0.019 |
| Biotope type | 4.93 | 0.293 |
| Season x biotope type interaction | 10.96 | 0.204 |
| **Family richness** | | |
| Season | 28.45 | <0.001 |
| Biotope type | 8.83 | 0.065 |
| Season x biotope type interaction | 14.48 | 0.070 |

### *3.3.2 Effect of season and biotope on assemblage structure*

PERMANOVA results indicate significant differences in parasitoid assemblages across biotopes (Pseudo-F=1.78, P=0.001) and over seasons (Pseudo-F=2.6284, P=0.001). There was also a significant interaction between biotope type and season's influence on parasitoid assemblages (Pseudo-F=1.45, P=0.001). During autumn, parasitoid assemblages differed between all biotope types, except for vineyards that did not differ significantly from old field and riparian assemblages (Fig. 3.2, Table 3.2). The CAP ordination indicates some overlap in parasitoid assemblages between vineyards and riparian as well as old field habitats (Fig. 3.2). These results are different to those of spring where there is greater dissimilarity in parasitoid assemblages across biotope types (Fig. 3.3, Table 3.3). Parasitoid assemblages for all biotope types differ significantly from one another (Table 3.3) with riparian assemblages appearing the most dissimilar from the other biotopes, grouping away from the other biotopes in the CAP ordination (Fig. 3.3). During late summer, parasitoid assemblages are more similar across biotopes (Fig. 3.4, Table 3.4). The only dissimilarity during this season is between riparian and

old field assemblages, with marginally significant dissimilarities between vineyard and natural, and vineyard and riparian parasitoid assemblages (Table 3.4). It is clear that there is a change in overall parasitoid assemblage structure from one season to the next. Additionally, similarities in parasitoid assemblages between biotope types for each respective season also varies over time. This indicates significant changes in parasitoid assemblage structure across the farmland mosaic over time.

These findings are further supported by Figure 3.5 (A-D) where CAP ordinations display parasitoid assemblages within various biotope types and how these assemblage structures differ over seasons. Assemblages within riparian habitats differ greatly between spring and summer, but are similar between autumn and summer. In contrast, vineyard, natural and old field habitats exhibit high dissimilarity in parasitoid assemblages between all 3 seasons. Invaded habitat assemblages are however highly similar between spring and summer (Table 3.5).

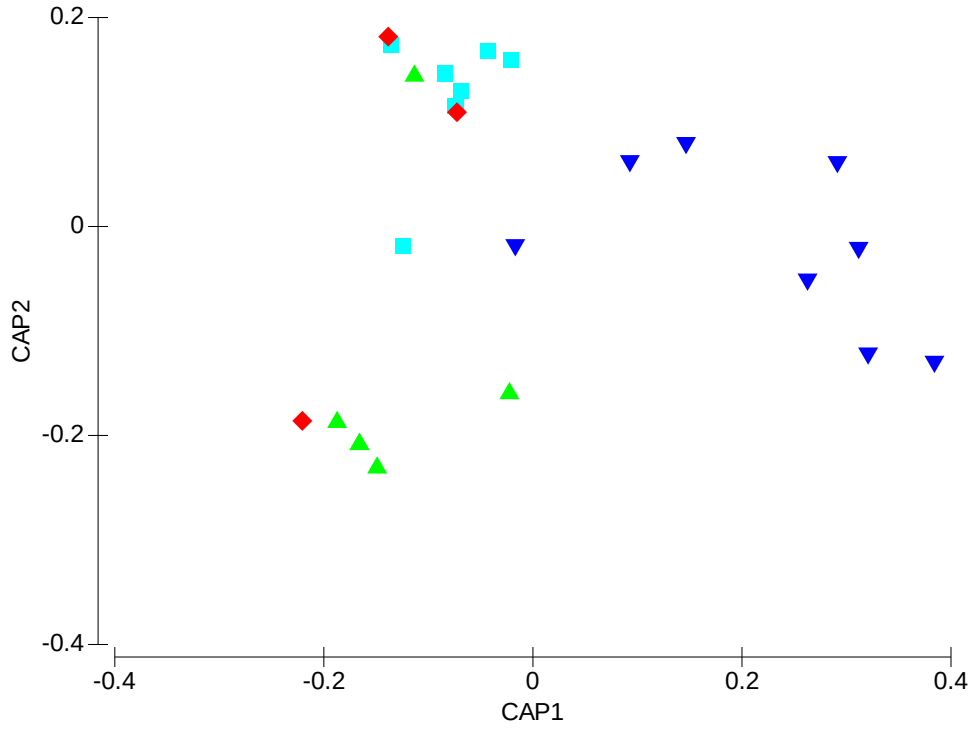


Figure 3.2: Ordination of CAP analysis indicating differences in parasitoid assemblage structure between biotopes for autumn. There was only one invaded site for this season and it was thus removed to avoid skewing of the dataset. The analysis was based on Bray-Curtis similarities and square root transformed abundance data. Green triangle= vineyard, blue triangle = natural, cyan square= old field, red diamond = riparian, purple circle = invaded.

Table 3.2: t-values of post-hoc pairwise comparisons from PERMANOVA analysis indicating significant differences between biotope types for autumn.

| | Vineyard | Natural | Old field |
|---|---|---|---|
| **Natural** | 1.3369* | | |
| **Old field** | 1.1471 | 1.492** | |
| **Riparian** | 1.1169 | 1.3912* | 1.2816* |

*P<0.05, **P<0.005, ***P<0.001

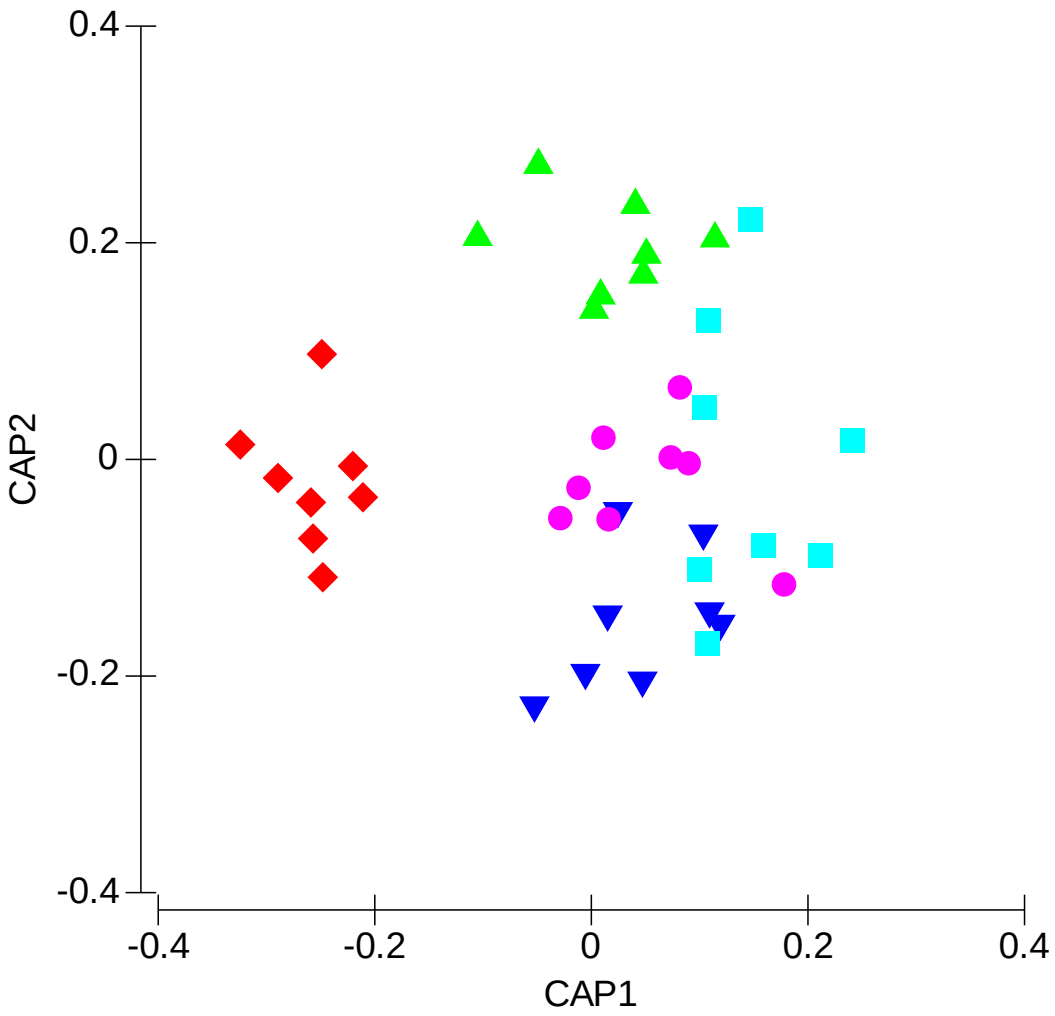


Figure 3.3: Ordination of CAP analysis indicating differences in parasitoid assemblage structure between biotopes for spring. Based on Bray-Curtis similarities derived from square root transformed parasitoid abundance data. Green triangle= vineyard, blue triangle = natural, cyan square= old field, red diamond = riparian, purple circle = invaded.

Table 3.3: t-values of post-hoc pairwise comparisons from PERMANOVA analysis indicating significant differences between biotope types for spring.

| | **Vineyard** | **Natural** | **Old Field** | **Riparian** |
|---|---|---|---|---|
| **Natural** | 1.6737*** | | | |
| **Old Field** | 1.2934* | 1.2627* | | |
| **Riparian** | 1.3884*** | 1.4612** | 1.3676*** | |
| **Invaded** | 1.3061*** | 1.2202* | 1.1109* | 1.2912*** |

*P<0.05, **P<0.005, ***P<0.001

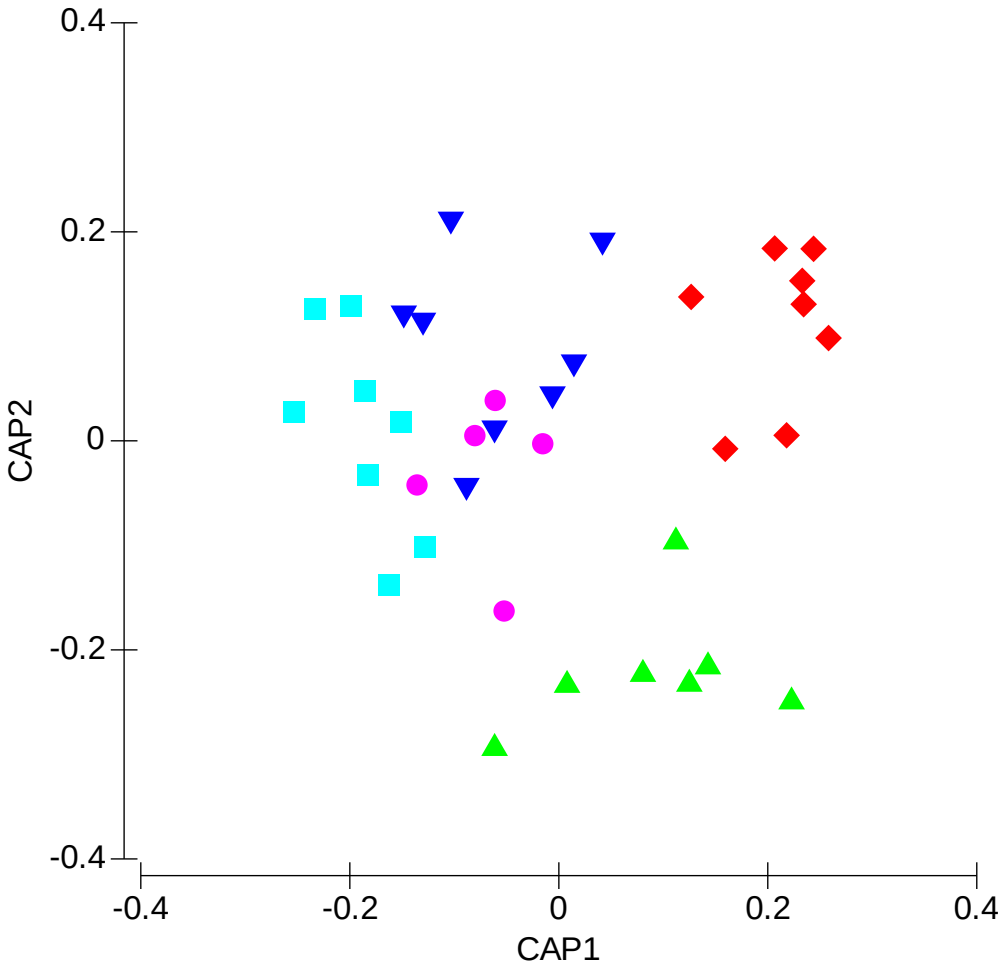


Figure 3.4: Ordination of CAP analysis indicating differences in parasitoid assemblage structure between biotopes for late summer. Based on Bray-Curtis similarities derived from square root transformed parasitoid abundance data. Green triangle= vineyard, blue triangle = natural, cyan square= old field, red diamond = riparian, purple circle = invaded.

Table 3.4: t-values of post-hoc pairwise comparisons from PERMANOVA analysis indicating significant differences between biotope types for late summer. Vineyard-natural (p=0.055), and vineyard-riparian (p=0.056) pairwise comparisons are marginally non-significant.

| | **Vineyard** | **Natural** | **Old field** | **Riparian** |
|---|---|---|---|---|
| **Natural** | 1.1970 | | | |
| **Old field** | 1.1357 | 1.1914 | | |
| **Riparian** | 1.2161 | 1.0839 | 1.3692** | |
| **Invaded** | 1.1131 | 0.8721 | 1.1902 | 1.0641 |

*P<0.05, **P<0.005, ***P<0.001

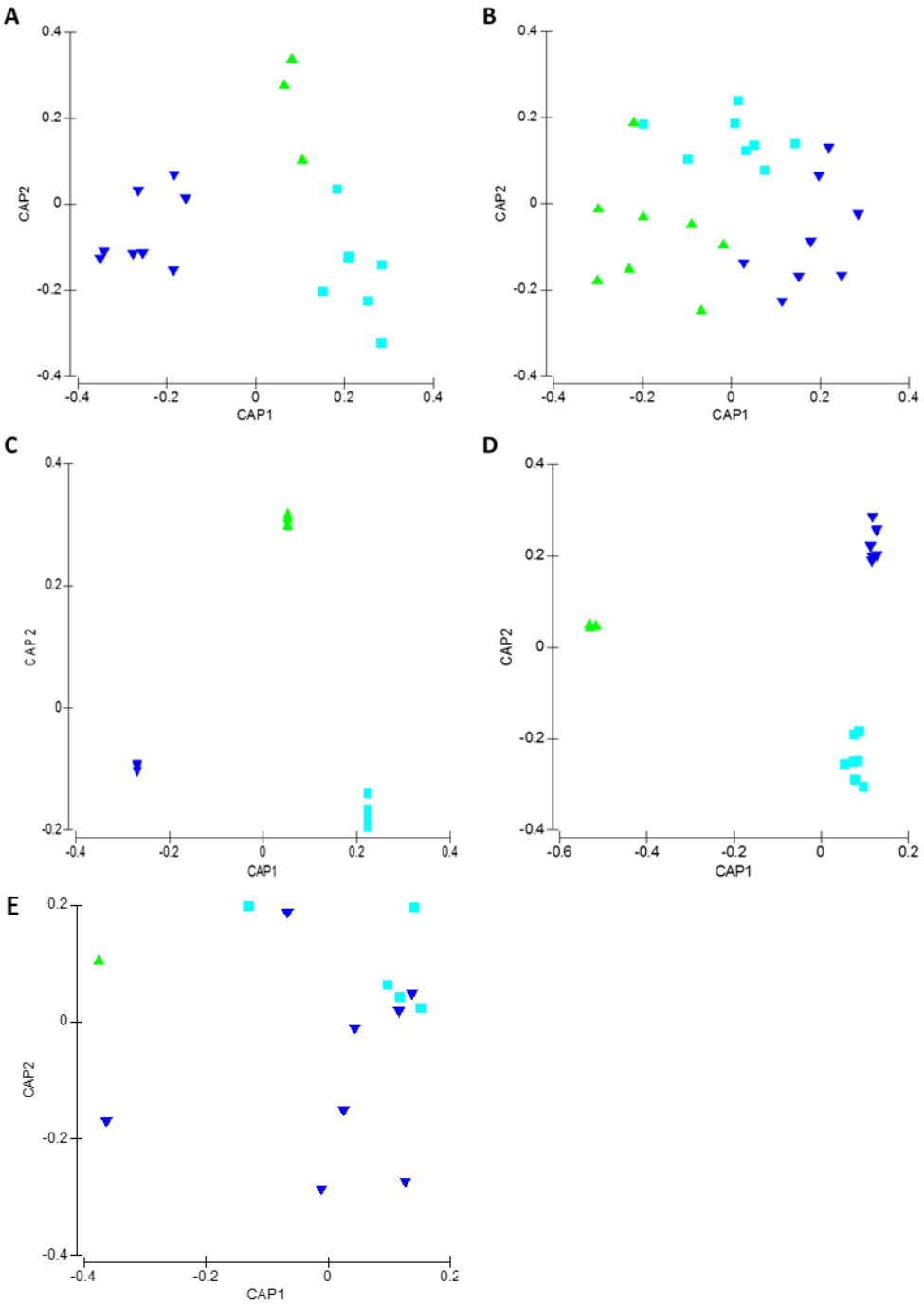


Figure 3.5: Ordination of CAP analysis indicating differences in parasitoid assemblage structure between seasons for A) Vineyard, B) Natural, C) Old field, D) Riparian and E) Invaded biotopes. Based on Bray-Curtis similarities and derived from square root transformed parasitoid abundance data. Green triangle= autumn, blue triangle = spring, cyan square= summer.

Table 3.5: t-values derived from PERMANOVA analyses with their respective levels of significance for each biotope type across seasons. There was only one invaded site in autumn and as a result it was removed.

| **Vineyard** | | Autumn | Spring | **Natural** | | Autumn | Spring |
|---|---|---|---|---|---|---|---|
| | Spring | 1.4003*** | | | Spring | 1.1981* | |
| | Summer | 1.3762* | 1.6751*** | | Summer | 1.2581* | 1.2433* |
| **Old field** | | Autumn | Spring | **Riparian** | | Autumn | Spring |
| | Spring | 1.4400*** | | | Spring | 1.3021* | |
| | Summer | 1.5057*** | 1.4465** | | Summer | 1.0869 | 1.3189*** |
| **Invaded** | | Spring | | | | | |
| | Summer | 0.9783 | | | | | |

*P<0.05, **P<0.005, ***P<0.001

## 3.4 Discussion

### *3.4.1 Spatiotemporal change of parasitoid assemblages*

Parasitoid assemblage structure varies across the farmland mosaic over time, suggesting that species move between various habitat types in response to changing environmental conditions. This is evident here as parasitoid assemblages sampled in one season differed from the next. The fact that I did not find an interaction effect, suggests that these seasonal changes are independent of the vegetation sampled. These findings are in accordance with Tylianakis et al (2005) who concluded that temporal as well as spatial dynamics are important for the distribution of biodiversity. Additionally, they found that the diversity of Hymenoptera within various habitat types varied greatly across seasons. If season one (autumn) of this study were to be examined alone, it would be clear that natural habitats support greater parasitoid abundance and richness compared to the other habitat types. However, when considering spring and late summer it becomes evident that riparian habitats are a vital component to the mosaic of habitat types found within agricultural landscapes. Multi-seasonal approaches are therefore essential to achieve more accurate findings about the movement of these highly mobile natural enemies.

Organisms are required to move between a range of crop and non-crop habitats within agricultural landscapes if they wish to survive (Tscharntke et al., 2005). Irregular distributions of plant resources and insect prey within agricultural systems force natural enemies to constantly search for alternative sources of food (Landis et al., 2005). Parasitoids move across the landscape in pursuit of resources and prey species. Small habitat fragments are essential for the survival of these high trophic-level specialists (Tscharntke et al., 2002), highlighting the importance of remnant natural and near-natural habitat patches as vital complementary sources of habitats for parasitoid populations.

Alternative non-crop habitats are especially important in agroecosystems where periods of extreme disturbance are experienced during times of harvest. Vineyard habitats exhibited low values of parasitoid abundance and richness during times of harvest (summer) and when the vineyards began to lose their leaves (autumn). It has been suggested that parasitoids may be required to leave crop habitats in search of resources, especially during overwintering periods (Bianchi et al., 2006). Recolonization of vineyards will then depend on the movement of natural enemies from other habitats (Wissinger, 1997). Studies have noted the invasion of natural enemies into arable fields along with the resultant decline in pest densities (Cardinale et al., 2003; Östman et al., 2003). Habitat connectivity becomes important as it enhances the dispersal of various natural enemies within agricultural landscapes (Landis et al., 2005).

Previous research whereby corridors were established near vineyards showed that natural enemies were provided with a constant supply of alternative food sources and in turn provided vineyards with consistent dispersal of generalist predators and parasitoids (Nicholls et al., 2001). Furthermore, Landis et al. (2005) stated that the presence of less disturbed habitats near crop fields may be important for the conservation of beneficial insects. Spatial and temporal patterns of resource availability influence the movement of natural predators within and around crop fields. Furthermore, the degree to which natural enemies spill-over into surrounding crop habitats after disturbance depends on the relative quality and distance of non-crop habitat patches within farmland mosaics (Cronin and Reeve, 2005; Bianchi et al., 2006). The turnover of species between habitat patches is essential within agricultural mosaics as it ensures the maintenance of overall arthropod diversity of the landscape (Tylianakis et al., 2005; 2006).

Parasitoid assemblages in riparian habitats differed greatly between spring and summer, but were similar between autumn and summer. Vegetation complexity along rivers may allow for the protection of arthropods from environmental changes during colder months, which explains the similarity in parasitoid assemblages between the hot and cold seasons in this study. The drastic dissimilarity in assemblage structure of riparian habitats between spring and summer may be due to arthropods using these habitats as refuges in response to the extreme heat and water shortages experienced within other habitat types during the summer. Although vineyards are usually regularly irrigated, riparian habitats may additionally provide shaded shelter from extreme heat during the summer months. There are however few studies to support this.

### *3.4.2 Conservation implications*

Here, this study indicates that habitat heterogeneity and patch isolation are important factors to consider when investigating species turnover across agricultural mosaics, which is in accordance with Tscharntke et al. (2007). A landscape perspective is necessary for the protection of beneficial arthropods and subsequent enrichment of biological control (Keijn and van Langevelde, 2006). Few studies have examined the movement of arthropods, especially parasitoids, between habitat patches over time and the drivers of these movements. The change in parasitoid assemblage structure at each biotope type for the different seasons emphasises that there is much more to discover about parasitoid movement across farmland mosaics over space and, more importantly, time. Future research should adopt a multi-seasonal approach when investigating natural enemy movement across and connectivity within agricultural landscapes. It is necessary to investigate why species move into certain habitat patches at a given time and the influence of these patterns on pest suppression. This will allow farm managers to more accurately plan not only the layout of the crop/non-crop mosaic, but also the timing of harvesting and sowing, to ensure the conservation of natural enemies.

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# Chapter 4

## 4.1 Conclusion

Here I show the need to maintain diverse agricultural mosaics within the Cape Floristic Region (CFR) in order to preserve diverse parasitoid assemblages and particularly unique species found within the various habitat types. Although natural habitats supported more diverse assemblages, the highly disturbed vineyard and invaded sites also make unique contributions to overall parasitoid diversity with similar patterns of species richness within dominant families in these patches (Chapter 2). Thus the entire landscape could be necessary for the maintenance of diverse and functionally complex parasitoid assemblages across farmland mosaics. Recognising undisturbed land as a priority for conservation, it is important to encourage heterogeneity across farmland mosaics.

High species richness enhances resilience within ecosystems by allowing for the co-existence of various species that respond differently to disturbance (Walker, 1995). When biodiversity is closely linked with the provision of ecosystem services and functioning, crop diversification improves resilience within agricultural systems (Lin, 2011). However, while agricultural intensification threatens farmland biodiversity, increasing diversity of habitats within agricultural landscapes can lessen this threat (Benton et al., 2003). Furthermore, protection of alternative habitat types within agricultural landscapes promotes arthropod survival. For example, habitat diversity increases diversity of generalist insects within crops (Jonsen and Fahrig, 1997).

The conservation of remnant patches within the CFR is therefore needed not only for the preservation of vast diversities of plants (Goldblatt and Manning, 2000) and arthropods (Procheş and Cowling, 2006), but also for the overall resilience of agricultural landscapes through conservation of biodiversity within these patches. Where individual habitats are too small to support sustainable arthropod populations, it becomes necessary to protect a network of habitat patches across landscapes for their long-term survival (Ekroos et al., 2016). Therefore, conservation of a diversity of habitat patches is important for arthropods within farmland mosaics (Smith et al., 2014).

Parasitoids are important natural enemies of agricultural pests (Pak et al., 2015; Pereira et al., 2007) and so are economically important to farmers, reducing reliance on chemical pest

control (Heraty, 2009). Various studies have identified parasitoid sensitivity to agricultural intensification and expansion (Andow, 1991; Bianchi et al., 2005; Gagic et al., 2011; Gonthier et al., 2014; Landis, et al., 2000; Marino and Landis, 1996), where habitat fragmentation and isolation negatively influences parasitoid diversity. Similarly, my study in the CFR found that the undisturbed natural and riparian patches supported highest parasitoid richness and diversity (Chapter 2). Furthermore, various studies have highlighted the importance of habitat complexity for parasitoids (Altieri et al., 2005; Danne et al., 2010; Landis et al., 2000; Nicholls et al., 2001; Pak et al., 2015; Randlkofer et al., 2010). My study is in accordance with these findings, as percentage natural vegetation and riparian area positively influenced parasitoid assemblages, with parasitoid species and family richness increasing with higher percentages of natural area.

The importance of non-crop vegetation within farmlands as sources of alternative prey and host species has been highlighted (Bianchi et al., 2006). For example, prune trees planted adjacent to vineyards were used by an important egg parasitoid specie of the genus *Anagrus* (Corbett and Rosenheim, 1996). Furthermore, Macfadyen and Muller (2013) emphasized the potential of natural remnants for increasing overall parasitoid population abundance across the landscape and ultimately improved parasitism of crop pests nearby. The value of nearby natural remnants as important habitats for parasitoids has been shown by various studies around the world (Aluja et al., 2014; Fraser et al., 2007) including in the CFR (Gaigher et al., 2015). Farm managers are therefore encouraged to preserve remnants near or adjacent to crop fields to promote parasitoid abundance and diversity in and around vineyards.

Where landscapes are fragmented and heterogeneous, as in agricultural mosaics, movement between patches could promote survival of both plants and animals (Wiens et al., 1993). Parasitoid assemblages varied significantly across seasons, indicating that patches exhibit varying degrees of importance for these organisms in response to changing environmental conditions (Chapter 3). The mosaic of resources available to parasitoids within agricultural landscapes changes throughout the year due to growth and harvesting of crops (Baudry and Papy, 2001; Rand et al., 2006). Parasitoids are then required to move across the landscape in search of vital resources, including host and prey species, to ensure their survival (Landis et al., 2000; Menalled et al., 1999).

These natural enemies not only require various types of patches, but movement between these patches seasonally. Patch connectivity becomes important in this situation, and depends on both the distance between patches and the occurrence of alternative patches that serve as stepping stones and corridors (Ricketts, 2001). Intermediate habitat types, such as old fields, may become important stepping stones, promoting connectivity between patches (Vrdoljak and Samways, 2013). This may be the case here as old fields shared the greatest number of parasitoid species with natural and riparian habitats (Chapter 2), suggesting significant species turnover between these biotopes.

### 4.2 Management Recommendations

It is evident here that parasitoids are highly influenced by both spatial and temporal factors, making it important for farmers to maintain a diversity of biotopes across agricultural landscapes to preserve these valuable natural enemies. This can be done by softening the matrix through the promotion of non-crop vegetation such as field margins and remnant patches (Bianchi et al., 2006). By promoting semi-natural vegetation within agricultural lands, farm managers may successfully enable the movement of organisms across farmland mosaics (Stamps et al., 1987).

A multi-seasonal approach, where the entire agricultural mosaic is taken into consideration, could be beneficial for conservation of these vital organisms. Research aimed at investigating the movement of parasitoid assemblages across biotopes will be beneficial for future farmland design. The value of conserving a mosaic of biotopes within agricultural landscapes may further be emphasized by learning more about the agriculturally important parasitoid species and their role as natural enemies of vineyard pests. By investigating the direct influence that specific parasitoid species have on specific agricultural pests, as well as the movement of these organisms in response to changing environmental conditions, farm managers may more accurately plan both the layout and timing of various farm practices.

### 4.3 Future Research

This study emphasizes the need to maintain a diversity of biotopes to preserve biodiverse parasitoid assemblages across agricultural landscapes. Agriculturally important parasitoid species were however, not taken into account here. Future research should focus on the relative abundance and diversity of agriculturally important parasitoid species to ensure

effective pest control within agricultural landscapes. Furthermore, by focussing on interactions between parasitoids and pest prey species, it may be inferred that parasitoids moving into arable fields are providing the important service of pest control (Furlong and Zalucki, 2010).

There is great need for research that adopts a landscape perspective along with a multi-seasonal approach. The crop mosaic changes from one year to the next (Burel and Baudry, 2005), resulting in the need for studies to be carried over longer time periods. By overlapping spatial and temporal scales in agricultural research, we may move closer to understanding the drivers behind species movement across the agricultural mosaic over time. Research focussed on patterns of species movement may allow us to discover which patches are important to natural enemies at certain times throughout agricultural cycles (Macfadyen and Muller, 2013). Such findings are especially important in the highly biodiverse and threatened CFR.

To promote biodiversity within the CFR, while simultaneously keeping up with the ever growing human population and subsequent expanding farm industry, it is essential for researchers to discover the relative importance of various biotopes within the farmland mosaic across seasons. Here, it is evident that a diversity of biotopes is beneficial for parasitoids. Furthermore, parasitoids move between habitats across seasons. The next step would be to investigate the exact drivers of this movement so that farm managers may fully understand the extent to which diverse mosaics benefit them not only economically, but also ecologically.

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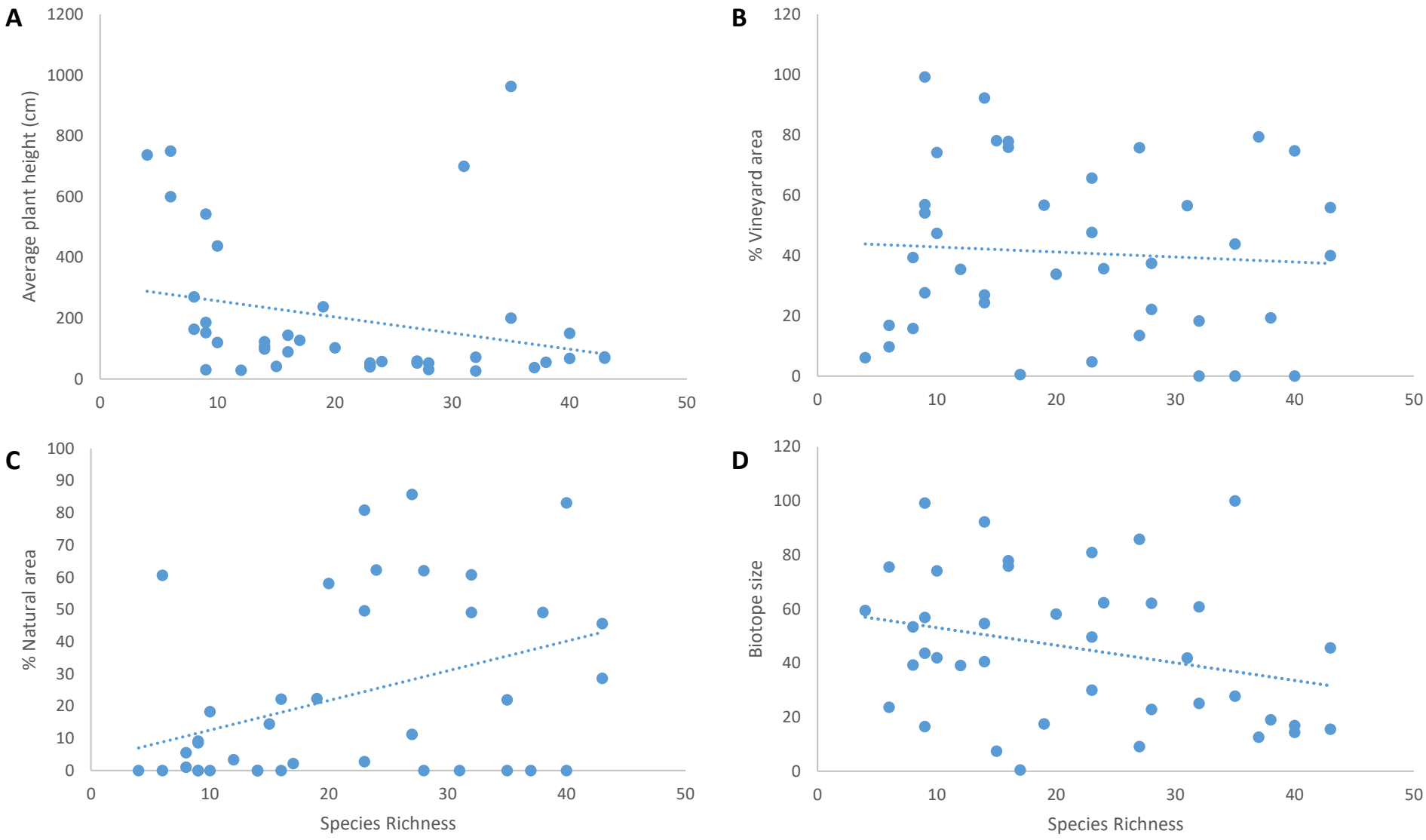
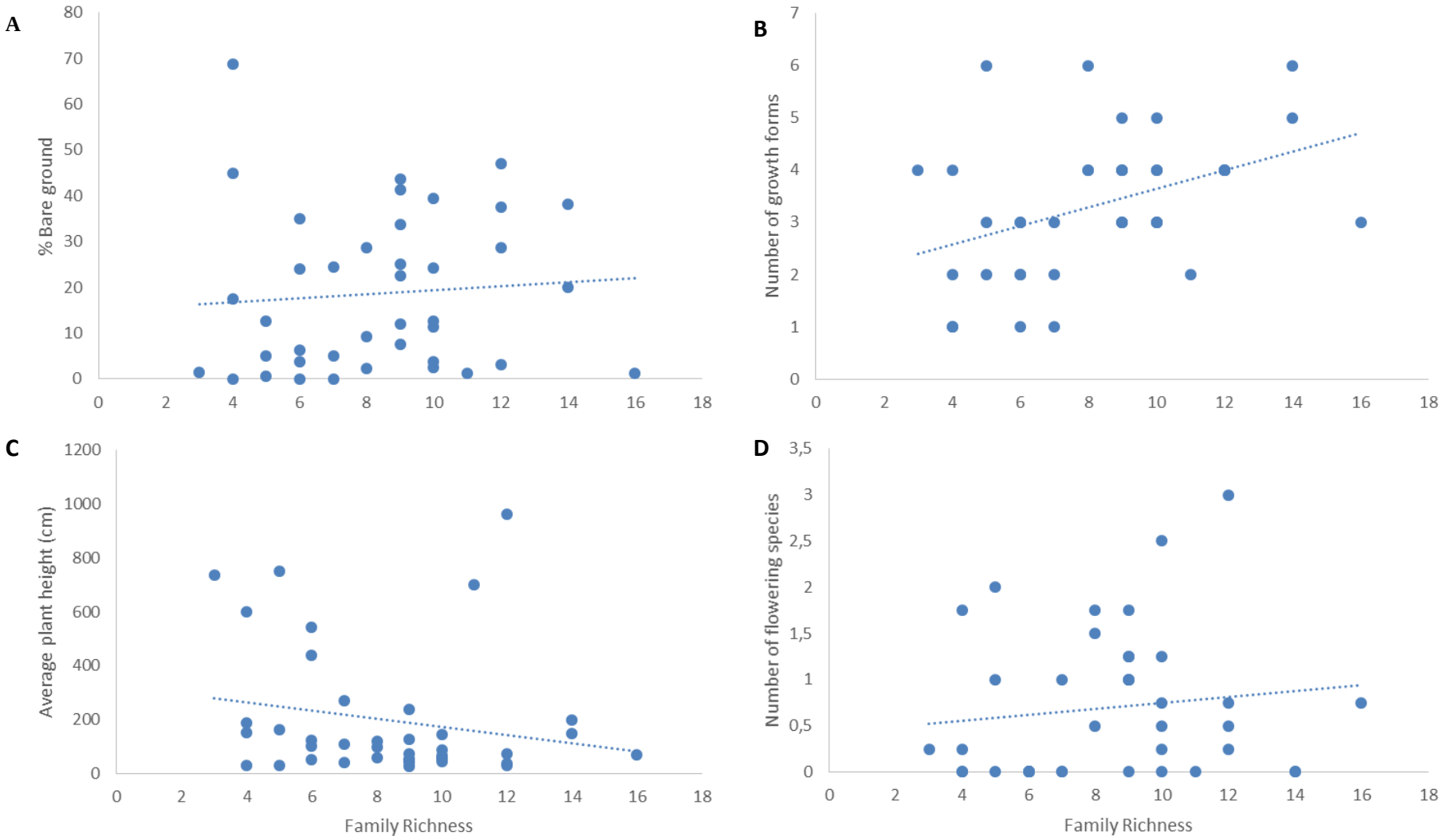
## Appendix A





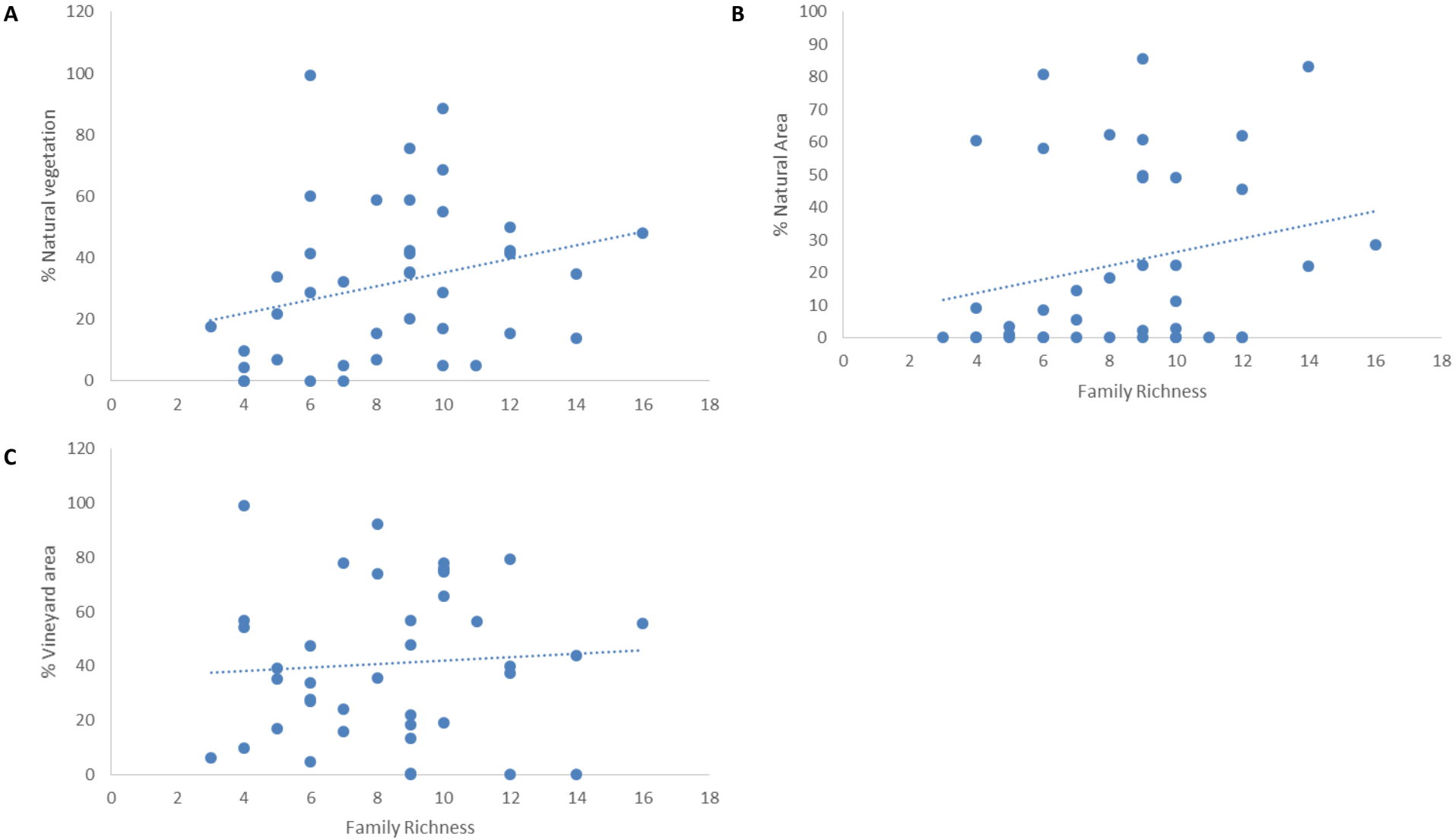

Significant correlations between parasitoid species richness and A) average plant height, B) percentage vineyard area, C) percentage natural area, and D) biotope size.

## Appendix B




Significant correlations between parasitoid family richness and A) percentage bare ground, B) number of growth forms, C) average plant height, and D) number of flowering species.

## Appendix C






Significant correlations between parasitoid family richness and A) percentage natural vegetation, B) percentage natural area, and C) percentage vineyard area.

## Appendix D

Parasitoid species richness of each family, in each biotope type.

| | Vineyard | Natural | Semi-Natural | Riparian | Invaded |
|---|---|---|---|---|---|
| Elasmidae | 1 | 0 | 1 | 3 | 1 |
| Ceraphronidae | 4 | 3 | 2 | 6 | 4 |
| Platygastridae | 12 | 18 | 17 | 27 | 15 |
| Braconidae | 11 | 20 | 16 | 36 | 7 |
| Eupelmidae | 2 | 4 | 6 | 3 | 2 |
| Signiphoridae | 0 | 1 | 0 | 0 | 0 |
| Aphelinidae | 0 | 5 | 3 | 6 | 2 |
| Eulophidae | 6 | 28 | 22 | 27 | 17 |
| Mymaridae | 2 | 7 | 10 | 5 | 2 |
| Trichogrammatidae | 0 | 3 | 2 | 1 | 1 |
| Eurytomidae | 5 | 8 | 2 | 5 | 2 |
| Pteromalidae | 11 | 12 | 15 | 11 | 6 |
| Encyrtidae | 6 | 14 | 13 | 13 | 7 |
| Chalcididae | 2 | 1 | 0 | 1 | 1 |
| Bethylidae | 0 | 4 | 2 | 1 | 2 |
| Figitidae | 4 | 1 | 2 | 9 | 1 |
| Diapriidae | 0 | 0 | 1 | 7 | 0 |
| Megaspilidae | 4 | 3 | 1 | 2 | 1 |
| Torymidae | 1 | 1 | 0 | 5 | 3 |
| Ichneumonidae | 1 | 1 | 1 | 3 | 0 |
| Proctotrupidae | 0 | 0 | 0 | 5 | 3 |
| Eucharitidae | 0 | 0 | 0 | 1 | 0 |
| Total | 72 | 134 | 116 | 177 | 77 |